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Chargé de recherche au Muséum d'histoire naturelle de Genève

Comité de lecture

Il est constitué en outre du président de la Société suisse de Zoologie, du directeur du Muséum de Genève et de représentants des instituts de zoologie des universités suisses.

Les manuscrits sont soumis à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: biogéographie, systématique, évolution, écologie, éthologie, morphologie et anatomie comparée, physiologie.

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Systematics and phylogenetic relationships of Whip snakes (*Hierophis* Fitzinger) and *Zamenis andreana* Werner, 1917 (Reptilia: Squamata: Colubrinae)

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Systematics and phylogenetic relationships of Whip snakes (*Hierophis* Fitzinger) and *Zamenis andreana* Werner, 1917. - Morphological and molecular data of *Coluber* (sensu lato) *andreas* and all recognised species of the Palearctic whip snake genus *Hierophis* Fitzinger are presented. Morphologically, *Andreas'* racer shows remarkable similarities to dwarf snakes (*Eirenis* spp., *Pseudocyclophis persicus*). Derived conditions of head and body pholidosis including dorsal scale reduction pattern and the number of apical pits separate *Eirenis* Jan and *C. (s.l.) andreas* from *Hierophis* spp. Character states strongly support sister group relationship of dwarf snakes to *Andreas'* racer. Molecular analyses confirm monophyly of *Hierophis* spp., *C. (s.l.) andreas*, and dwarf snakes of the genus *Eirenis*, and paraphyly of *Hierophis* auct. MtDNA sequences indicate a basal position of the eastern Palearctic *H. spinalis* vis-à-vis the western species group (*H. cypriensis*, *H. gemonensis*, *H. viridiflavus*). These taxa belong to an early radiation within whip and dwarf snakes. The eastern Mediterranean *H. caspius*, *H. jugularis*, and *H. schmidt* appear to represent a paraphyletic grouping including *C. (s.l.) andreas* (12S rDNA sequence data). Conflicting molecular and morphological results are discussed and the character phylogeny of external morphological features is re-assessed.

Key-words: *Coluber (s.l.) andreas* - *Eirenis* - *Hierophis* - morphology - osteology - hemipenis - transformation series - phylogeny - mtDNA.

INTRODUCTION

Without taking account of Oriental taxa (Utiger, 2002), Old World racers and their allies belong to at least eight different genera, i.e., *Eirenis* Jan, 1863, *Hemorrhphis* Schätti & Utiger, 2001, *Hemorrhphis* Boie, 1826, *Hierophis* Fitzinger in Bonaparte, 1834, *Lytorhynchus* Peters, 1862, *Platycephalus* Blyth, 1860, *Pseudocyclophis* Boettger, 1888, and *Spalerosophis* Jan, 1865 (Schätti 1986, 1987; Schätti & Utiger, 2001). The latter genus is the sister taxon of *Hemorrhphis* Boie. Together with *Platycephalus* Blyth, they make up a monophyletic group among Old World racers.

The Palaearctic whip snake (or racer) genus *Hierophis* Fitzinger belongs to a distinct evolutionary lineage within Afrotropical, Palaearctic, and Saharo-Sindian racers. It is considered to include *H. caspius* (Gmelin, 1789), *H. cypriensis* (Schätti, 1985), *H. gemonensis* (Laurenti, 1768), *H. jugularis* (Linnaeus, 1758), *H. schmidtii* (Nikolskij, 1909), *H. spinalis* (Peters, 1866), and *H. viridiflavus* (Lacépède, 1789), the type species (Schätti, 1987, 1988, 1993; Schätti & Utiger, 2001; Utiger & Schätti, 2004).

Zamenis andreana Werner, 1917 from the southern Zagros Mountains in Iran is a poorly known and enigmatic species characterised by a number of distinctive external morphological features typically encountered in dwarf snakes of the genus *Eirenis* Jan. Schätti (2001) thought that Andreas' racer is a representative of an early evolutionary lineage among Palaearctic racers. Schätti & Utiger (2001) placed the taxon in their *incertae sedis* section, i.e., *Coluber sensu lato*, stressing the necessity of comparison with *Eirenis* spp.

A preliminary molecular analysis (Schätti & Utiger, 2001) generated low bootstrap values for the European (*Hierophis gemonensis*, *H. viridiflavus*) and eastern Mediterranean (*H. caspius*, *H. jugularis*, *H. schmidtii*) whip snakes. On the basis of mtDNA sequence data, *Eirenis modestus* (Martin, 1838) turned out to be the sister taxon of the latter species group, thus rendering *Hierophis* auct. paraphyletic. The reality of two whip snake groups was also confirmed with cytochrome b sequences (Nagy *et al.*, 2000).

Using external morphological characters, vertebra (only *Hierophis* spp.) and hemipenis features, as well as molecular methods, this study investigates the phylogenetic relationships of *Zamenis andreana* Werner, the systematic composition of *Hierophis*, and the morphological demarcation of whip snakes vis-à-vis dwarf snakes, i.e., *Eirenis* spp. and *Pseudocyclophis persicus* (Anderson, 1872).

MATERIAL AND METHODS

Methods and definitions of terms used in the text are explained in Schätti (1987, 1988). For the purpose of this study, the number of anterior suboculars may include an additional (supplementary) scale. The anterior temporals are made up of the first and second row of scales. Bilateral reductions of the number of longitudinal dorsal scale rows (dsr, at midbody: msr) are either low (lateral) or high (i.e., paravertebral or vertebral). Their position on the posterior portion of the trunk is expressed as a percentage of the total number of ventrals (%ven) and calculated on the basis of the average of the right and left side counts. Vertebra measurements, and in particular the length of the centrum (lc) and neural crest (nc), the least width of the neural arch (wn), and the width across the prezygapophyses (wp), are figured in Helfenberger (2001).

Scientific names of *Hierophis* spp. are cited with the author and year of publication upon their first mention in the text. In the case of *Eirenis* spp. except those used for molecular analyses (see below), as well as Oriental racer genera cited in the Discussion, only the author's name is given.

Acronyms used in the text are CAS (California Academy of Sciences, San Francisco), MHNG (Muséum d'histoire naturelle, Genève), MVZ (Museum of Vertebrate Zoology, Berkeley), and ZMUC (Zoologisk Museum, København).

Hierophis Fitzinger (sensu Utiger & Schätti, 2004) is understood to contain two European taxa, the endemic Cyprus whip snake, three eastern Mediterranean species, as well as the eastern Palaearctic *H. spinalis*. Lacépède's whip snake (*H. viridiflavus*) from NE Spain to Dalmatia, Malta, and Gyaros Island (Cyclades) in the Aegean Sea, the Balkans whip snake (*H. gemonensis*) from Dalmatia to the Aegean region, and *H. cypriensis* make up the western species group. Eastern Mediterranean species include *H. caspius* from the Balkans eastward and two Anatolia-Caucaso-Iranian species, *H. jugularis* and *H. schmidtii*. As to the systematic make-up of dwarf snakes, the reader is referred to the appropriate section in the text.

External morphological data for *Coluber* (s.l.) *andreas* are from five specimens reported earlier (Schätti, 2001) and MHNG 2626.59. Scale features of *Eirenis* and *Hierophis* spp. are from Boulenger (1894, 1914), Eiselt (1976), Schmidtler & Schmidtler (1978), Docenko (1985), Schätti (1985, 1987, 1988), Docenko (1989), Franzen & Sigg (1989), Schmidtler & Eiselt (1991), Böhme (1993), Schätti (1993), Schmidtler (1993), Schmidtler & Baran (1993b), Schmidtler (1997), Sivan & Werner (2003), and Utiger & Schätti (2004).

A partial sequence of the mitochondrial small ribosomal subunit (12S rRNA) of six racer or dwarf snake taxa and presumably related colubrids was obtained from frozen muscle or a dry skin (*Eirenis* sp.). Voucher specimens are *Coluber* (s.l.) *andreas* (Werner, 1917) MHNG 2626.59 (Iran: Gavilah, Khuzestan), *Eirenis medus* (Chernov in Terentjev & Chernov, 1940) MHNG 2627.4 (Iran: vicinity of Mahniyah, Hamadan/Zanjan border), *E. punctatolineatus* (Boettger, 1892) MHNG 2626.99 (Iran: vicinity of Hashtijan, Fars), *Eirenis* sp. MHNG 2626.71 (Iran: Mehkuyeh, Fars; sloughed skin, see Dwarf Snakes), *Lytrochynchus diadema* (Duméril, Bibron & Duméril, 1854) MHNG 2427.32 (Yemen: Jabal Mafluq), and *Spalerosophis microlepis* Jan, 1865 MHNG 2626.70 (Iran: Mehkuyeh, Fars).

The technique of DNA isolation as well as PCR and sequencing procedures are described in Utiger *et al.* (2002). The obtained data were added to a selection of 16 Palaearctic, Saharo-Sindian, and an Oriental racer species from an existing sequence file consisting of two partially analysed mitochondrial genes, cytochrome oxidase subunit I (COI) and 12S rRNA (Utiger & Schätti, 2004). Due to constraints in laboratory facilities, only one gene region (12S rRNA) was investigated for the new taxa presented in this study. The lacking COI characters were coded as missing.

Phylogenetic analyses were performed with PAUP* version 4.0b10 for Mac (Swofford, 1998). Weighted maximum parsimony (MP) procedures are described in Utiger *et al.* (2002) and Utiger & Schätti (2004). Gaps in the 12S rDNA sequence were treated as fifth character state. After a first run with heuristic search and tree-bisection reconnection (TBR) branch swapping, characters were weighted with the rescaled consistency index (RC, Farris, 1989) and a second heuristic search was performed. The procedure was repeated once; further weighting did not alter the parameters of the resulting tree. Nonparametric bootstrap values (Felsenstein, 1985) with 1000 replicates were calculated for unweighted and weighted characters.

TABLE 1. Sequence properties and tree reconstruction parameters

	gaps: missing unweighted MP	gaps: 5 th character state unweighted MP	character state weighted MP
Length of sequence alignment (COI/12S)	1017 (407/610)	1017 (407/610)	1017 (407/610)
Total of variable characters (COI/12S)	339 (142/197)	350 (142/208)	350 (142/208)
- parsimony-informative ((COI/12S)	249 (116/133)	256 (116/140)	256 (116/140)
Number of most parsimonious trees	4	2	1
Tree length	1067	1121	266.72
Rescaled consistency index (RC)	0.195	0.199	0.478

RESULTS

Hierophis Fitzinger, 1834

Loreal and preocular single (the latter rarely divided). Usually eight supralabials (seven to nine), fourth and fifth entering eye. Anterior subocular situated between third and fourth supralabial; sometimes very small or, rarely, lacking in *Hierophis jugularis*; occasionally absent or with an additional small scale in *H. spinalis*. Two postoculars, normally only upper in contact with parietal. Usually two (one to, sometimes, three) scales in first row of temporals, and two or three (rarely one) in second. Nine or ten (eight to twelve) sublabials (Tb. 3).

Ventrals in ♂♂ 163-174 (*gemonensis*) and 178-211, ♀♀ 168-182 and 194-227, respectively; subcaudals 86-125 (♂♂) and 84-117 (♀♀). Maximum total length ca. 100 cm (*cypriensis*, *gemonensis*, *spinalis*) to over 200 cm (*caspius*, *jugularis*).

TABLE 2. Selected morphological data for *Hierophis* spp. Dorsal scale rows (dsr) on the neck, at midbody, and prior to the vent, posterior reduction pattern (prp: low (l) or high (h), see Material and Methods), number of maxillary (max), palatine (pal), pterygoid (pter), and dentary (den) teeth as well as vertebrae ratios (length of the centrum: lc, length of neural crest: nc, least width of neural arch: wn, width across prezygapophyses: wp).

Species	dsr	prp	max	pal	pter	den	lc/wn	lc/wp	nc/wn
<i>caspius</i>	17-19-15	1 - l(-h)	12-15	9	14-18	14-17	1.25-1.44	0.70-0.77	0.88-1.05
<i>cypriensis</i>	17-17-13	1 - h	16-18	10-11	17-20	19-20	1.38-1.58	0.74-0.80	1.11-1.28
<i>gemonensis</i>	17-19-15	1 - l	16-19	9-12	20-23	16-23	1.23-1.35	0.70-0.74	0.95-1.03
<i>jugularis</i>	17-19-15	1 - l	12-14	11	18-20	16-20	1.16-1.36	0.71-0.73	0.94-1.04
<i>schmidtii</i>	17-19-15	1 - l	12-15	9	17-19	14-17	1.36-1.39	0.72-0.75	1.00-1.08
<i>spinalis</i>	17-17-15	1	13-15	8-10	10-12	16-18	1.45-1.53	0.74-0.81	1.05-1.21
<i>viridiflavus</i>	17-19-15	1 - l	14-16	9-11	15-20	15-18	1.28-1.44	0.68-0.82	0.88-1.05

Dorsal scales with paired apical pits, in 17 longitudinal rows at neck (15th ventral), 17-19 msr, and 13-15 in front of vent. A lateral increase of the number of dsr on anterior portion of trunk except in *Hierophis cypriensis* and *H. spinalis*. One (*spinalis*) or two lateral reductions involving rows 2-5 on both sides of posterior portion of body; a third fusion (rows 6-8), in most cases unilateral (i.e., 14 dsr prior to vent), sometimes occurs in *H. caspius*. *H. cypriensis* has 17 dsr throughout the

TABLE 3. Selected morphological characters in *Hierophis* spp. (*caspius*, *gemonensis*, *jugularis*, *schmidtii*, *viridiflavus*), *H. cypriensis*, *H. spinalis*, *Coluber* (s.l.) *andreaus*, *Eirenis* spp. (*africanus*, *aurolineatus*, *barani*, *collaris*, *coronella*, *coronelloides*, *deceimlineatus*, *eiselti*, *hakkariensis*, *levantinus*, *medius*, *modestus*, *rechingeri*, *rothi*, *thospitis*), *E. lineomaculatus*, *E. p. punctatolineatus*, and *Pseudocyclophis* (*P. persicus*). Number of loreal, preocular (preoc), anterior subocular (suboc, see Material and Methods), supralabial (supral), sublabial (sublab, *; see Results), postocular (postoc, *; sometimes single in *E. medius*), and anterior (first and second) temporal (temp) scales, apical pits (a.p.), longitudinal scale rows at midbody (msr), and posterior reduction pattern (prp: low (l), high (h), or no fusion (0), see Material and Methods). Unusual conditions in parenthesis.

Taxa	loreal	preoc	suboc	supral	sublab	postoc	1st temp	2nd temp	a.p.	msr	prp
<i>Hierophis</i> spp.											
<i>H. cypriensis</i>	1	1 (2)	1 (0)	8 (7,9)	9-10 (*)	2	2 (1,3)	2-3	2	19	1-l(-h)
<i>H. spinalis</i>	1	1	1	8 (9)	10	2	2 (1)	2-3	2	17	1-h
<i>C. (s.l.) andreaus</i>	1	1	1 (0,2)	8 (9)	9 (8,10)	2	2 (1,3)	2-3	2	17	1
<i>Eirenis</i> spp.											
<i>E. lineomaculatus</i>	1	1	0-2	7	8	2	1	2 (1)	1	17	1 or 0
<i>E. punctatolineatus</i>	0 (1)	1 (2)	0	7	7-8 (9)	2 (1*)	1	2 (1)	1	15-17	1 or 0
<i>Pseudocyclophis</i>											
<i>E. lineomaculatus</i>	1	1	0	7	8 (7)	1 (2)	1	2 (1)	1	17	1
<i>E. punctatolineatus</i>	1	1	0	7	9 (8,10)	2	1	2	1	17	1
<i>Pseudocyclophis</i>	0 (1)	1	0	7	8	1 (2)	1	1	1	15	1 or 0

forebody, a first reduction involving the third and fourth row at 61-68%ven, and a paravertebral or vertebral reduction (rows 6+7 or 7+8) to 13 dsr situated between 66-79%ven (Tbs 2-3).

Maxillary with 12-19 teeth, palatinum 8-12, pterygoid 10-12 (*spinalis*) and 14-23, and dentary 14-23. Vertebra ratios are: lc/wn 1.16-1.58, lc/wp 0.68-0.82, nc/wn 0.88-1.28 (Tb. 2).

Hemipenis with 3-6 distinct rows of spines; enlarged basal hook present in *Hierophis cypriensis*, *H. gemonensis*, and *H. spinalis*. Apex calyculate and bulbous in everted state (two longitudinal grooves *in situ*); borders of calyces denticulate proximally, usually smooth towards apex.

Coluber (sensu lato) *andreaeus* (Werner, 1917)

Pl. 1

Loreal and preocular single. Seven supralabials, third and fourth in contact with eye. Anterior subocular single, paired, very small, or absent (Schätti, 2001: Tb. 1; one



PLATE 1

Coluber (sensu lato) *andreaeus* (♀) MHNG 2626.59 from Khuzestan (Gavilah), Iran.

distinct subocular in MHNG 2626.59). Two postoculars, both (lower only partially) in contact with laterally extended parietal. First temporal single, coalesced with sixth supralabial in ZMUC R6044 (Schätti, 2001: Fig. 1)¹, usually two (one) scales in second temporal row. Eight sublabials (Tb. 3).

¹ Erroneously stated to be fused with the parietal (Schätti, 2001).

Ventrals show a pronounced sexual dimorphism, i.e., 217-218 (two ♂♂) and 247-269 (four ♀♀); subcaudals 92-96 and 84-94, respectively. Maximum total length 445+155 mm (♂) and 586+164 mm (♀) in syntypes (Werner, 1917).

Dorsal scales with single apical pits (best visible on flanks), in 17 longitudinal rows on anterior portion of trunk and at midbody, and 17 (no reduction) or 15 dsr in front of vent (Schätti, 2001). CAS 100474 (♂) with a lateral reduction involving row 2+3 at 87%ven; MHNG 2626.59 (♀) has 17-15-17 (etc.) dsr between ventrals 221-246 (89-99%ven), fluctuation between rows 2-4, and row 1+2 in the case of the last reduction to 15 dsr.

Maxillary with 9-13 teeth (10 in MHNG 2626.59). Proximal portion of hemipenis spinose (no further data available, vertebra ratios unknown).

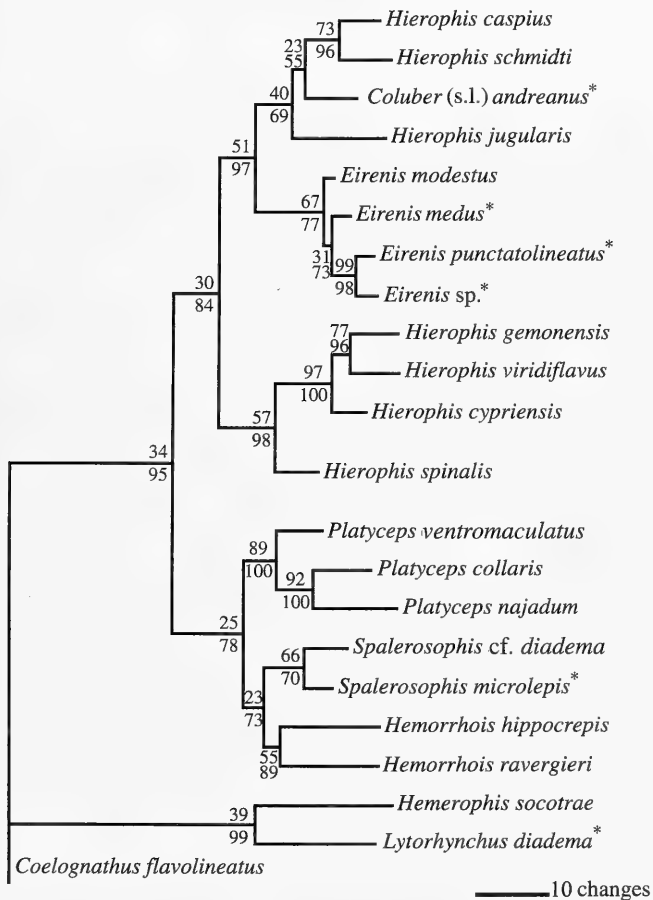


FIG. 1

Weighted maximum parsimony (MP) tree of two partially sequenced gene regions (COI and 12S RNA) with the Oriental racer *Coelognathus flavolineatus* (Schlegel) as outgroup. In the case of taxa with an asterisk reconstruction is based on 12S rDNA sequence data only. Bootstrap values (1000 replicates) from unweighted (upper) and weighted (lower values) MP analysis.

COMPARATIVE MORPHOLOGY

Coluber (s.l.) *andreas* differs from *Hierophis* spp. in lower supralabial and sublabial counts (7 instead of 8 and 8 vs. usually 9-10, respectively), parietal shape, i.e., laterally extended and in contact with lower postocular, and a single first temporal scale (parietal usually not reaching beyond upper postocular, 2 first temporals)², 247 or more ventrals in females (227 or less), single apical pits (paired), only one lateral dsr reduction that is sometimes absent (invariably present, Tb. 3), and a maximum total length of ca. 75 cm vs. 100-200 cm or more. Andreas' racer possesses a surprising number of external morphological character states in common with *Eirenis* spp. (see Tbs 3-4 and Discussion).

Hierophis cypriensis differs from congeneric species in, for instance, the occurrence of a paravertebral or vertebral reduction on the posterior portion of the trunk (Utiger & Schätti, 2004), and it has the highest lc/wn and nc/wn ratio within the genus (Tbs 2-3).

Due to similar osteological (basisphenoid) and hemipenis features (bulbous shape and general ornamentation), the senior author assumed that *Masticophis spinalis* Peters from Central Asia to Korea belonged to *Hierophis* (Schätti, 1987: Figs 1, 3.e; Schätti, 1988: Figs 6, 8). *H. spinalis* is exceptional among Palaearctic whip snakes in only one reduction on the posterior portion of the trunk involving lateral scale rows, low tooth counts of the pterygoid (Tb. 2), and coloration, i.e., presence of a light vertebral stripe and no ontogenetic change of the dorsal colour pattern.

The geographically isolated *Hierophis spinalis* and *H. cypriensis* differ from congeneric species in, for instance, a lower number of dsr (17 instead of 19) on the forebody (Tb. 2), presence of a basal hook (also in *H. gemonensis*, see Character Phylogeny), the shape of the lateral processus of the pterygoid (simple instead of bicuspid), and higher vertebra ratios (lc/wn, nc/wn, Schätti, 1987: Fig. 2). It also appears that female *H. spinalis* attain larger maximum size than males, whereas the contrary applies to congeneric species except *H. cypriensis*.

DWARF SNAKES

As generally understood (e.g., Doczenko, 1985; Leviton *et al.*, 1992), dwarf snakes contain the putatively monotypic genus *Pseudocyclophis* Boettger, i.e., *P. persicus* (Anderson) (including, e.g., *P. walteri* Boettger) reported from eastern Anatolia to Pakistan, as well as *Eirenis* Jan. *Eirenis africanus* (Boulenger) from NE Sudan to Djibouti (and probably NW Somalia) as well as 16 valid species from the eastern Mediterranean area to the Caucasus, Iran, and Turkmenistan are recognised, i.e., *E. aurolineatus* (Venzmer), *E. barani* Schmidtler, *E. collaris* (Ménétriés), *E. coronella* (Schlegel), *E. coronelloides* (Jan), *E. decemlineatus* (Duméril, Bibron & Duméril), *E. eiselti* Schmidtler & Schmidtler, *E. hakkariensis* Schmidtler & Eiselt, *E. levantinus* Schmidtler, *E. lineomaculatus* Schmidt, *E. medus* (Chernov), *E. modestus* (Martin), the type species (Schmidtler & Schmidtler, 1978), *E. punctatolineatus* (Boettger), *E.*

² The antero-lateral extension of the parietal, and its contact with the lower postocular, is correlated with the condition of the first temporal scale (single).

rechingeri Eiselt, *E. rothi* (Jan), and *E. thospitis* Schmidtler & Lanza. Nine *Eirenis* spp. (53%) were described or revalidated (*E. coronelloides*) over the last 33 years.

Pseudocyclophis persicus attains a total maximum length of ca. 50 cm and is characterised by the usual absence of a loreal (small if present) and a single postocular (Tbs 3-4). *P. persicus* has 15 msr and sometimes a posterior dsr reduction, 2 (1+1) anterior temporals, a slender habitus as well as high ventral (up to 224 in ♂♂, 238 in ♀♀) and subcaudal counts (95 and 85, respectively, Doczenko, 1985).

Doczenko (1989) assigned *Eirenis collaris*, *E. coronella*, *E. eiselti*, *E. medus*, *E. rechingeri*, and *E. rothi*, i.e., species with 15 msr except *E. africanus* (not examined), to a new subgenus, *Collaria*. Schmidtler & Eiselt (1991) noted that, for instance, the closely related *E. hakkariensis* and *E. thospitis* with 17 and 15 msr, respectively (see below), caused considerable doubt ("erhebliche Bedenken") as to the taxonomic division of *Eirenis* Jan, and later studies (e.g., Schmidtler, 1993: 94) called the validity of *Collaria* into question. Finally, the close relationship ("nahe Verwandtschaft") of *E. modestus* (17 msr) with *E. thospitis* induced Schmidtler (1997) to abandon Doczenko's (1989) subgeneric concept.

Nine of the 17 species including *Eirenis coronelloides* and *E. thospitis* have 15 msr and there is no posterior dsr reduction except in *E. coronella* (fide Schmidtler & Schmidtler, 1978) and *E. africanus* (Ineich, 2003)³.

Eirenis collaris, *E. eiselti*, *E. medus*, and *E. rothi* make up the "*E. collaris* group" (e.g., Schmidtler & Baran, 1993a) that may have evolved from *E. modestus* ("Linie *E. modestus* - *E. collaris* - *E. rothi*", Schmidtler, 1993) or from a common ancestor stock (Schmidtler, 1997). A single postocular sometimes occurs in *E. medus* (Tb. 3). *E. rothi* often has only 7 sublabials and a single second temporal, i.e., only 2 instead of usually 3 anterior temporals. In this species, the shape of the parietal (see footnote 2) is a variable feature as exemplified by MHNG 1247.1 (borders lower postocular) and MHNG 1363.58 (only in contact with upper postocular).

Single second temporals are normally also found in *Eirenis coronella*. This small species (ca. 35 cm maximum total length) sometimes has 9 sublabials, a reduction from 15 (msr) to 13 dsr in front of the vent, and low ventral (125 in ♂♂, 143 in ♀♀) and subcaudal counts (Schmidtler & Schmidtler, 1978; Sivan & Werner, 2003). *E. coronelloides* is a minuscule (ca. 25 cm maximum total length) eastern Mediterranean (southern Levant) species. It has few ventrals (♂♂ 123-134, ♀♀ 140-155) and subcaudals (36-48 and 33-40, respectively) and differs from *E. coronella* (40-67 subcaudals) in "having a black crown, a dark ventral stripe or both" (Sivan & Werner, 2003). In the latter species, Schmidtler & Schmidtler (1978) recorded a minimum of 32 subcaudals for females and 38 in male specimens.

The phylogenetic affinities of *Eirenis africanus*, *E. coronella*, *E. coronelloides*, and the singular *E. rechingeri* (striped, only known from the holotype) remain unclear. *E. africanus* is rare in collections; this species has 2 (1+1) anterior temporals (Boulenger, 1914) but, according to Scortecci (1930: Fig.), the parietal does not touch the lower postocular (see footnote 2).

³ This character state could not be ascertained for *Eirenis thospitis* and *E. coronelloides*. In the latter species, it is supposed that there is no difference vis-à-vis *E. coronella*, i.e., that *coronelloides* has a reduction to 13 dsr prior to the vent.

The “*Eirenis modestus* complex” (sensu Schmidtler, 1997) includes *E. thospitis* with 15 msr and five species (*aurolineatus*, *barani*, *hakkariensis*, *levantinus*, and *modestus*) with 17 msr and, usually, a reduction to 15 dsr prior to the vent (see footnote 3).

The posterior reduction may be present or absent in *Eirenis aurolineatus* and *E. levantinus*. *E. modestus* has exceptionally (“sehr selten”, Schmidtler & Baran, 1993b) 19 msr; this number is more often found in *E. m. cilicius* Schmidtler from around Burdur, Turkey (Schmidtler, 1997). Specimens of *E. modestus* with 17 dsr at midbody and in front of the vent (i.e., no reduction) are documented (e.g., Schmidtler & Eiselt, 1991; Schmidtler, 1993: Tb. 1).

A considerable number (33%, n=13) of northern Anatolian *Eirenis m. modestus* examined by Schmidtler (1997) have a single postocular and, rarely, there are 2 temporals in the first row (Schmidtler & Baran, 1993b). All taxa of the “*E. modestus* complex” show variation in the number of preoculars (1-2), although two scales are uncommon in *E. levantinus* and *E. hakkariensis* (Schmidtler & Eiselt, 1991: Tb. 1; Schmidtler, 1993: Tb. 1)⁴. The latter species is comparatively large (ca. 50 cm maximum total length) and has 8-9 sublabials. Schmidtler & Eiselt (1991) discuss differences of the Hakkari dwarf snake and *E. punctatolineatus* (see below).

Eirenis lineomaculatus with a posterior reduction from 17 to 15 dsr involving lateral rows is among the smallest species (ca. 30 cm maximum total length, Schmidtler & Schmidtler, 1978) of the genus (see *E. coronelloides*). *E. lineomaculatus* is outstanding for a usually single postocular and absence of the loreal, or its small size if present (Tbs 3-4), as well as extremely low ventral (103-119 in ♂♂, 117-132 in ♀♀) and subcaudal (28-38 and 21-33, respectively) counts (Schmidtler & Schmidtler, 1978).

Eirenis decemlineatus and *E. punctatolineatus* possess a posterior reduction from 17 to 15 dsr involving lateral rows. The latter is remarkable for an elevated number of sublabials (9, sometimes 10) in the nominate subspecies (Tbs 3-4); *E. p. kumerloevii* Eiselt sometimes has 8 sublabials (Eiselt, 1976: Tb.; Franzen & Sigg, 1989: Tb. 1). *E. decemlineatus*, with a total length of up to 90 cm by far the largest dwarf snake, has 7-9 sublabials and may have 3 second temporals. Schmidtler & Eiselt (1991) noted that these species are probably not closely related (“vermutlich nicht einmal näher miteinander verwandt”), and that the intraspecific (“geographische”) variation of *E. decemlineatus* requires further studies.

A sloughed skin of an *Eirenis* sp. from Fars Province (Iran, see Material and Methods) lacked the anteriormost portion (including head) and tail tip and could not be identified with certainty. Given the length of the fragment (ca. 65 cm), 17 msr, and clear genetic differences vis-à-vis *E. punctatolineatus* (Fig. 1), it cannot be excluded that the exuvia is from *E. decemlineatus*. Eiselt (1971) noted that this species had not yet been recorded from the vicinities of Shiraz.

The dwarf snake fauna of Iran is not yet well explored as exemplified by *Eirenis medus* (see Material and Methods). It appears that Eiselt's (1971) reference to *E. decemlineatus* and the presence of this species in “Iran” as noted by Leviton *et al.* (1992) rely on Wall's (1908) “*Contia*

⁴ Most probably, the alleged absence of a preocular in certain specimens of *Eirenis barani* and *E. levantinus* (Schmidtler, 1993: Tb. 1) is in error.

decemlineata" from Maidan Mihaftan (Masjed Soleyman, Khuzestan). The specimens having "In the posterior part [...] spots [that] become rearranged in longitudinal interrupted lines" most probably belong to *E. punctatolineatus*. This pattern is unknown in *E. decemlineatus* (F. J. Schmidtler in litt. August 2003).

CHARACTER PHYLOGENY

Schätti (2001) regarded the outstanding features of *Coluber* (s.l.) *andreas*, i.e., the low number of supralabial, sublabials, and temporal scales, the occasional absence of an anterior subocular, few dsr, and the absence of posterior reductions (or a single fusion involving paraventral rows) as probably ancestral character states ("wahrscheinlich plesiomorphe Merkmalszustände"). Mostly single preoculars, two supralabials entering the orbit, and the absence of high (paravertebral or vertebral) dsr reductions in most species led Schätti & Utiger (2001) consider *Hierophis* a conservative genus vis-à-vis other Palaearctic as well as Saharo-Sindian and Afrotropical racers and allied genera (*Hemorrhois*, *Platycephalus*, and *Spalerosophis* spp.). Although molecular (mtDNA) data of the type species of *Eirenis* Jan (*E. modestus*) suggested sister group relationship of dwarf snakes to eastern Mediterranean *Hierophis* spp., the authors put forward putatively ancestral conditions of external morphology in dwarf snakes, in particular the absence of an anterior subocular and few supralabial and temporal scales.

Schmidtler & Eiselt (1991) considered *Eirenis modestus* with 17 msr a very conservative ("sehr ursprüngliche") species. Taxa with 15 msr and including mostly small-sized ("eher kleinwüchsig") species were thought to be more advanced ("fortschrittliche") dwarf snakes (Docenko, 1989; Schmidtler, 1993: 90). New studies using multivariate analyses (Schmidtler, 1993, 1997) suggest that *E. decemlineatus*, the largest dwarf snake, is a very conservative and systematically isolated taxon ("extreme Außengruppe", Schmidtler, 1993: 93).

According to Schmidtler (1997), a large loreal ("großes Frenale") and high degree of fragmentation of the temporals ("hoher Zerfallgrad der Temporalia") are derived character states. This assertion collides with results showing that *Pseudocyclophis persicus* (loreal absent, 1+1 anterior temporals) is a highly advanced species (see Discussion) as evidenced by an extremely low reduction index (19, Schmidtler, 1993: Tb. 3). The third presumably advanced ("wohl synapomorphe") condition within dwarf snakes, i.e., the contact of the first temporal with the supralabial bordering the orbit ("häufiger Kontakt 1. Temporale und suboculares Supralabiale", Schmidtler, 1997: 49), is purely quantitative and highly variable. In the "*Eirenis modestus* complex", for instance, values range from 0% in *E. m. modestus* and certain populations of *E. m. semimaculatus* (Boettger) to 39% in *E. aurolineatus* (Schmidtler, 1997: Tb. 1, character 15).

In dwarf snakes, the loss ("Verschwinden") of the loreal (in *Eirenis lineomaculatus* and *Pseudocyclophis persicus*), the number of posterior (!) temporals, and in particular the cranial shift of the dsr reduction from 17 to 15 are correlated with the reduction of total length ("reduktionsrelevante Merkmale"). Dwarfism ("Verzwergung") also affects the diameter of the eye, width of the frontal, dimensions of the anterior and posterior inframaxillary scales, and, in males, the number of subcaudals.

The number of preocular, postocular, and gular scales are not influenced by this phenomenon (Schmidtler, 1997).

Without anticipating the situation in *Hemierophis socotrae* (Günther), the genera *Hemorrhais*, *Platycephs*, and *Spalerosophis*, as well as the unassigned racers *Coluber* (s.l.) *dorri* (Lataste), *C.* (s.l.) *scortecii* (Lanza), and *C.* (s.l.) *zebrinus* (Broadley & Schätti) from the western Sahel (Sudanese Arid), Somalia, and Namibia, respectively (see Schätti & Utiger, 2001), the morphological and molecular data presented in this study, and in particular the phylogenetic affinities of *C.* (s.l.) *andreas* and *Eirenis* spp., suggest character polarities for Palaearctic whip and dwarf snakes as listed in Table 4.

TABLE 4. Distribution of character states in dwarf and whip snakes. Taxa and their abbreviations are *Coluber* (s.l.) *andreas* (A), *Eirenis lineomaculatus* (B), *E. p. punctatolineatus* (C), *Eirenis* spp. (D, see Tb. 3), *Hierophis caspius*, *H. jugularis*, and *H. schmidt* (E), *H. gemonensis* and *H. viridiflavus* (F), *H. cypriensis* (G), *H. spinalis* (H), and *Pseudocyclophis persicus* (I). Characters (0 for ancestral, 1 for derived condition) are (1) loreal: present (0), absent (1); (2) postocular(s): paired (0), single (1); (3) subocular: present (0), absent (1); (4) sublabials: 9 or more (0), 7 or 8 (1); (5) supralabials: 8 or more (0), 7 (1); (6) first temporal(s): paired (0), single (1); (7) second temporal(s): 2 or 3 (0), single (1); (8) midbody dorsal scale rows: 19 (0), 15-17 (1); (9) posterior reduction(s): 2, rarely 3 (0), 1 or absent (1); (10) apical pits: paired (0), single (1). Conditions found in 95% or more of the individuals per species are shown; not considered are, in particular, the occasional occurrence of a single postocular in *E. medus* (Tb. 3) or rare character states found in other *Eirenis* spp., e.g., a single postocular and two first temporals (*modestus*) or the occasional presence of 9 sublabials (*decemlineatus*, *hakkariensis*, see Dwarf Snakes).

no.	character	A	B	C	D	E	F	G	H	I
1	loreal	0	1	0	0	0	0	0	0	1
2	postocular(s)	0	1	0	0	0	0	0	0	1
3	anterior subocular	0/1	1	1	1	0	0	0	0 (1)	1
4	sublabials	1	1	0 (1)	1	0	0	0	0	1
5	supralabials	1	1	1	1	0	0	0	0	1
6	first temporal(s)	1	1	1	1	0	0	0	0	1
7	second temporal(s)	0 (1)	0 (1)	0	0 (1)	0	0	0	0	1
8	midbody scale rows	1	1	1	1	0	0	1	1	1
9	posterior reduction(s)	1	1	1	1	0	0	0	1	1
10	apical pits	1	1	1	1	0	0	0	0	1

Stickel (1951) and Doczenko (1985: Fig.) studied hemipenis features of *Eirenis modestus* and dentigerous bones (palatinum, pterygoid) of *E. collaris*, *E. modestus* auct., and *Pseudocyclophis persicus*. However, published information about phylogenetically significant osteological (skull, vertebrae) and hemipenis characters are lacking for most dwarf snake species and *Coluber* (s.l.) *andreas*. According to Sivan & Werner (2003), Shwayat (1998) investigated "hemipenis morphology" of Jordan *Eirenis* spp.

The striking resemblance of *Hierophis jugularis*, *H. viridiflavus*, *Eirenis modestus* (and possibly other dwarf snake species), and Palaearctic ratsnakes as, for instance, *Elaphe schrenckii* Strauch and *Zamenis longissimus* (Laurenti) with respect to hemipenis ornamentation and its bulbous shape (Schätti, 1988: Figs 6-7; Schmidtler & Baran, 1993b: Fig. 55; Utiger *et al.*, 2002: Fig. 5) is most probably based on ancestral

character states. This is also the case with the enlarged basal spine found in *Hierophis* spp. (*cypriensis*, *gemonensis*, *spinalis*), *E. modestus*, and ratsnakes, e.g., *Zamenis lineatus* (Camerano) and species of the genera *Euprepiophis* Fitzinger and *Oreophis* Utiger, Helfenberger & Schätti.

DISCUSSION

Without taking account of the Oriental racer genera *Coelognathus* Fitzinger, *Gonyosoma* Wagler (including, e.g., *Herpetodryas frenatus* Gray and *Coluber prasinus* Blyth), and *Ptyas* Fitzinger (see Utiger, 2002), our molecular approach (Fig. 1) reveals three major evolutionary lineages of Old World colubrids. They are represented by five Palaearctic and Saharo-Sindian genera (*Eirenis*, *Hemorrhois*, *Hierophis*, *Platyceps*, *Spalerosophis*), Saharo-Sindian leaf-nosed snakes (*Lytorhynchus* spp.), and the Socotra racer (*Hemerothis socotrae*). The uncorrected sequence divergence (p) for 12S rDNA of *H. socotrae* and *Lytorhynchus diadema* is 14%, and, for instance, 10% in the case of *H. socotrae* and *Hierophis viridiflavus*.

The geographically isolated Namibia racer *Coluber* (s.l.) *zebrinus* belongs to a lineage that diverged from the common racer stock prior to the evolution of Afrotropical, Palaearctic, and Saharo-Sindian racers and related genera (Schätti & Charvet, 2003). The sequence divergence (p) vis-à-vis *Hemerothis socotrae* and *Hierophis viridiflavus* is 14.5% and 12%, respectively (unpubl. data).

Whip snakes of the genus *Hierophis* (sensu Utiger & Schätti), *Coluber* (s.l.) *andreas*, and *Eirenis* spp. are monophyletic (Fig. 1). They represent a distinct evolutionary lineage probably including *Pseudocyclophis persicus*.

MtDNA sequences corroborate preliminary molecular data (12S and COI rDNA) for *Eirenis modestus* and the phylogenetic affinities of dwarf snakes, paraphyly of *Hierophis* (sensu Utiger & Schätti), close relationship of *H. cypriensis*, *H. gemonensis*, and *H. viridiflavus*, and sister group status of the western whip snakes to the eastern Palaearctic *H. spinalis* (Schätti & Utiger, 2001; Utiger & Schätti, 2004). Furthermore, the phylogenetic tree (Fig. 1) indicates an early separation of western *Hierophis* spp. from a common ancestor stock giving rise to Palaearctic whip and dwarf snakes and suggests that *Eirenis* spp. are the sister group of *Coluber* (s.l.) *andreas* and the eastern Mediterranean *H. caspius*, *H. jugularis*, and *H. schmidtii*.

With regard to external morphology, European and eastern Mediterranean *Hierophis* spp. show ancestral character states. Most of these species are remarkable for large body size. The smaller *H. cypriensis* and *H. spinalis* are advanced whip snakes on the basis of low msr. The absence of an increase of dsr on the forebody in these taxa (present in congeneric species) is correlated with the number of msr. The single posterior dsr reduction and, rarely, the absence of an anterior subocular in *H. spinalis* are derived conditions.

Apart from Oriental genera (see above), *Hierophis caspius* and *H. jugularis* are the largest Old World racers. The reduction of body size is a remarkable evolutionary trend in Palaearctic whip and dwarf snakes affecting various scale characters as exemplified by the small *Eirenis lineomaculatus*, but not the minuscule *E. coronelloides* (see Dwarf Snakes and Character Phylogeny).

Character state distribution within the ingroup (Tb. 3) suggests that para-vertebral and/or vertebral dsr reductions found in *Hierophis cypriensis* may be derived

conditions. However, the occurrence of high reductions in *H. caspius* (Schätti, 1988) and the criterion of the correlation of transformation series (Hennig, 1979) might favour the opposite view. In the case of the presence of a light vertebral stripe in *H. spinalis*, the outgroup criterion within whip and dwarf snakes supports autapomorphy for this character state. This might also be true for larger female maximum size of *H. spinalis* or the distinct sexual dimorphism of ventral scales in *Coluber* (s.l.) *andreas*. Coloration features including melanism in Mediterranean *Hierophis* spp. are possibly correlated with large body size.

Based on the conditions in *Eirenis collaris*, *E. modestus*, and *Pseudocyclophis persicus* (Docenko, 1985: Fig.), the shape of the lateral process of the pterygoid in *Hierophis cypriensis* and *H. spinalis* (see Comparative Morphology) may be derived states. The character phylogeny of other osteological conditions found in these species, i.e., high lc/wn and nc/wn ratio, or few pterygoid teeth in *H. spinalis*, are difficult to assess for the lack of comparative material.

On higher systematic levels, the slow evolving 12S rDNA generally provides better results than the protein-coding COI sequence. Although 12S sequence data (Fig. 1) suggest paraphyly of eastern Mediterranean *Hierophis* spp., we consider the generic allocation of *Coluber* (s.l.) *andreas* as debatable. Reservations concerning the association of Andreas' racer with these whip snakes stem from morphological evidence, i.e., a considerable number of derived character states supporting sister group relationship of Andreas' racer to dwarf snakes.

Coluber (s.l.) *andreas*, *Eirenis* spp., and *Pseudocyclophis persicus* have a low number of supralabial (third and fourth bordering eye), sublabial (except *E. p. punctatolineatus*), and anterior temporal scales, the parietal in contact with the lower postocular (see footnote 2), 15-17 msr with single apical pits (Boulenger 1894; Böhme, 1993), and at most one posterior dsr reduction involving lateral or paraventral rows (Tbs 3-4). The occasional absence of an anterior subocular in *C. (s.l.) andreas* is the normal condition encountered in dwarf snakes. Furthermore, the maximum total length of these taxa does not exceed 100 cm.

Assuming the character phylogeny determined for whip and dwarf snakes (Tb. 4), an evolutionary history as indicated by molecular data (Fig. 1) would imply parallelism in *Coluber* (s.l.) *andreas* and *Eirenis* spp., or postulate reversal of the polarity in at least six transformation series (sublabials, supralabials, first temporal, msr, dsr reduction, and apical pits) in both eastern Mediterranean whip snake sections, i.e., *Hierophis jugularis* and *H. caspius - schmidtii*.

Derived conditions of head pholidosis including the occasional absence of an anterior subocular in *Coluber* (s.l.) *andreas* as well as derived dorsal scale features (few msr, at most one posterior dsr reduction, low reduction levels, and single apical pits) advocate monophyly of Andreas' racer, *Eirenis* spp., and *Pseudocyclophis persicus*. The occurrence of few body scale rows (dsr, msr) and lateral (low) reductions in *Hierophis spinalis* are due to parallelism.

Certain derived character states met with in *Coluber* (s.l.) *andreas*, e.g., the absence of a dsr reduction or only 2 (1+1) anterior temporals, are characteristic for *Eirenis africanus*, *E. coronella*, *E. rothi*, and *Pseudocyclophis persicus*. The latter species, morphologically the most strongly advanced dwarf snake, and the minute *E.*

lineomaculatus are distinguished by the absence of a loreal and single postoculars (synapomorphies). Remarkably, *P. persicus* and *C. (s.l.) andreanus* are similar in, for instance, their slender habitus and comparatively high ventral and subcaudal counts.

The dilemma posed by conflicting morphological and molecular data in *Coluber (s.l.) andreanus* calls for field work and further investigation in the laboratory. Certainly, paraphyly of the eastern Mediterranean *Hierophis* spp. and, hence, parallelism in Andreas' racer and *Eirenis* spp. as evidenced by mtDNA sequences cannot be excluded. From the molecular point of view, the systematic position of *C. (s.l.) andreanus* requires confirmation because a non coding sequence (12S rDNA) from a single specimen was analysed, i.e., a nuclear origin cannot be ruled out.

The examination of hemipenis and osteological characters, and more genetic information for *Coluber (s.l.) andreanus* and dwarf snake species such as *Eirenis africanus*, *E. coronella*, *E. lineomaculatus*, and *Pseudocyclophis persicus* are crucial for the understanding of the perplexing results presented in this study and the evolution of morphological characters including body size in Palearctic whip and dwarf snakes.

Taxonomic decisions with regard to Andreas' racer and the paraphyletic whip snake genus *Hierophis* (sensu Utiger and Schätti) are postponed pending further studies.

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Three new species of the genus *Gammarus* from tributaries of the Ili River, China (Crustacea, Amphipoda, Gammaridae)

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Three new species of the genus *Gammarus* from tributaries of the Ili River, China (Crustacea, Amphipoda, Gammaridae).

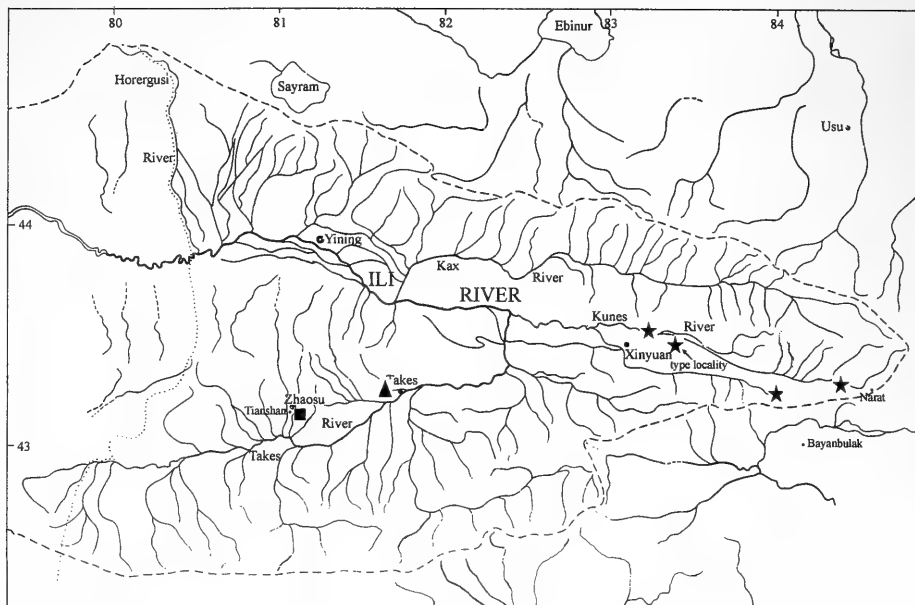
- Three new species of the genus *Gammarus* are described on the base of specimens collected from Ili River, Xinjiang, China. *Gammarus montanus* sp. n. is characterized by uropod 3 armed with long simple setae and antenna 2 lacking calceoli; *G. brevipodus* sp. n. is distinguished by the peduncle of antenna 2 with long setae along both margins and inner ramus of uropod 3 about one-third of outer ramus. *G. takesensis* sp. n. differs from *G. brevipodus* sp. n. by inner ramus of uropod 3 reaching three-fourths of outer ramus. Distribution data on these gammarids are also presented.

Key-words: Amphipoda - *Gammarus* - taxonomy - Ili River - China.

INTRODUCTION

The Ili River, also called “Yili” or “Ile” River, runs through parts of China and Kazakhstan. This river is 950 km long, rising from Mt Tianshan (NW Xinjiang of China) and flowing west across the China-Kazakhstan border, through the sandy Sary-Ishik-Otrau Desert, into Lake Balkhash. In its upper reaches the Ili is a mountain river; in the Balkhash plane it is a valley river. Before running into Lake Balkhash, it forms a delta of about 9000 km². Ili is famous for its beauty and attracts more and more visitors every year. In the course of an invertebrate survey of Mt. Tianshan, a collection trip along the Chinese part of the Ili River was made by Dr Zhixiao Liu and students from Xinjiang University in July and August 2001. When checking this collection, we found three new gammarids, which are described in the present paper. The relationship between the new species and other related gammarids is discussed and their known distribution is presented (Map 1).

Gammarus is one of the largest genera of epigean freshwater amphipods. Barnard & Barnard (1983) reviewed the freshwater Amphipoda worldwide and 117 species were listed under the genus *Gammarus*. After 1983, more than 20 species have



MAP 1. Localities of freshwater amphipods along the Chinese part of Ili River. Square = *Gammarus montanus* sp. n., triangle = *G. takesensis* sp. n., star = *G. brevipodus* sp. n.

been reported by several authors (Karaman & Pinkster, 1987; Barnard & Dai, 1988; Morino & Whitman, 1995; Stock *et al.*, 1998; Hou & Li, 2002a, b, c, 2003a, b, c, d; Hou, Li & Koenemann, 2002; Hou, Li & Morino, 2002; Hou, Li & Zheng, 2002; Meng, Hou & Li, 2003). According to the study by Karaman and Pinkster (1977a, b, 1987), these species can be subdivided into three artificial species groups, as shown in the key below. In the present paper, *Gammarus montanus* sp. n. belongs to the *G. pulex*-group, while *G. brevipodus* sp. n. and *G. takesensis* sp. n. belong to the *G. balcanicus*-group.

KEY TO SPECIES-GROUPS IN THE GENUS *GAMMARUS*

- 1 Metasome segments with middorsal process (carina). *G. roeseli*-group
- Metasome segments without middorsal process 2
- 2 Pereopods 3 and 4 and uropod 3 bearing numerous long setae . *G. pulex*-group
- Pereopods 3 and 4 and uropod 3 poorly setose *G. balcanicus*-group

MATERIAL AND METHODS

Specimens were collected by a net and then preserved in 75% alcohol. For each species three to five specimens of each sex were dissected and appendages were mounted on slides according to the methods described by Holsinger (1967). The drawings were made with the aid of a drawing tube mounted on an Olympus BX-41 compound microscope.

All holotypes treated in this study are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS), Beijing, China. Paratypes are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing (IZCAS), and in the Muséum d'histoire naturelle, Geneva (MHNG).

DESCRIPTIONS

Gammarus montanus sp. n.

Figs 1-5

Material: holotype, male (IZCAS-I-A0053), Tianshan Town, Zhaosu County (43.1°N, 81.1°E), collected by Dr Zhixiao Liu and Mr Ayiheng, August 12, 2001. Paratypes: 20 males, 20 females and 10 juveniles (IZCAS), 9 males and 9 females (MHNG), same data as for the holotype.

Etymology: the species name “*montanus*” refers to the habitat of this new species.

Diagnosis: *Gammarus montanus* sp. n. belongs to *Gammarus pulex*-group and is characterized by uropod 3 armed with long simple setae and by antenna 2 lacking calceoli.

Description of male: body 10.2 mm in length.

Head: eyes ovate, inferior antennal sinus deep (Fig. 1A).

Antenna 1 (Fig. 4A): peduncular articles 1-3 in length ratio 1 : 0.59 : 0.41, with slender setae distally; primary flagellum twenty-eight articulate, most articles with aesthetascs, accessory flagellum four articulate.

Antenna 2 (Fig. 4B): peduncular article 4 about as long as article 5, both with two to three groups of setae along anterior and posterior margins; flagellum ten articulate, calceoli lacking.

Upper lip convex, with minute setules (Fig. 1G).

Mandibles (Figs 1I, K): left incisor with five teeth, lacinia mobilis with four dentitions, molar with one long plumose seta; article 2 of palp with thirteen long stiff slender setae on medial margin, article 3 reaching 83% length of article 2, bearing two groups of long B-setae on medial surface, three long A-setae on lateral surface, a row of eighteen short plumose D-setae and four long E-setae. Right incisor with four teeth, lacinia mobilis bifurcate, molar with one long plumose seta.

Lower lip (Fig. 1H): inner lobe absent.

Maxilla 1 asymmetrical (Figs 1J, L): medial margin of inner plate bearing several slender setules basally, and fifteen plumose setae evenly distributed between the base and apex; outer plate sparsely setose medially, the apex bearing eleven serrate robust setae; palp two articulate, the left second article falcate, bearing eight naked robust setae apically accompanied by three stiff setules apico-facially; the right second article bearing five broad-based tooth setae and two stiff slender setae.

Maxilla 2 (Fig. 1F): inner plate with an oblique row of thirteen plumose setae on medial surface, evenly distributed between the base and apex; outer plate with stiff setae apically.

Maxilliped (Fig. 1M): inner plate bearing one subapical and three apical blade-like tooth setae, associated with plumose setae on medial and apical margins; outer plate bearing sixteen blade-like robust setae on medial margin and eight apical pectinate setae; palp four articulate.

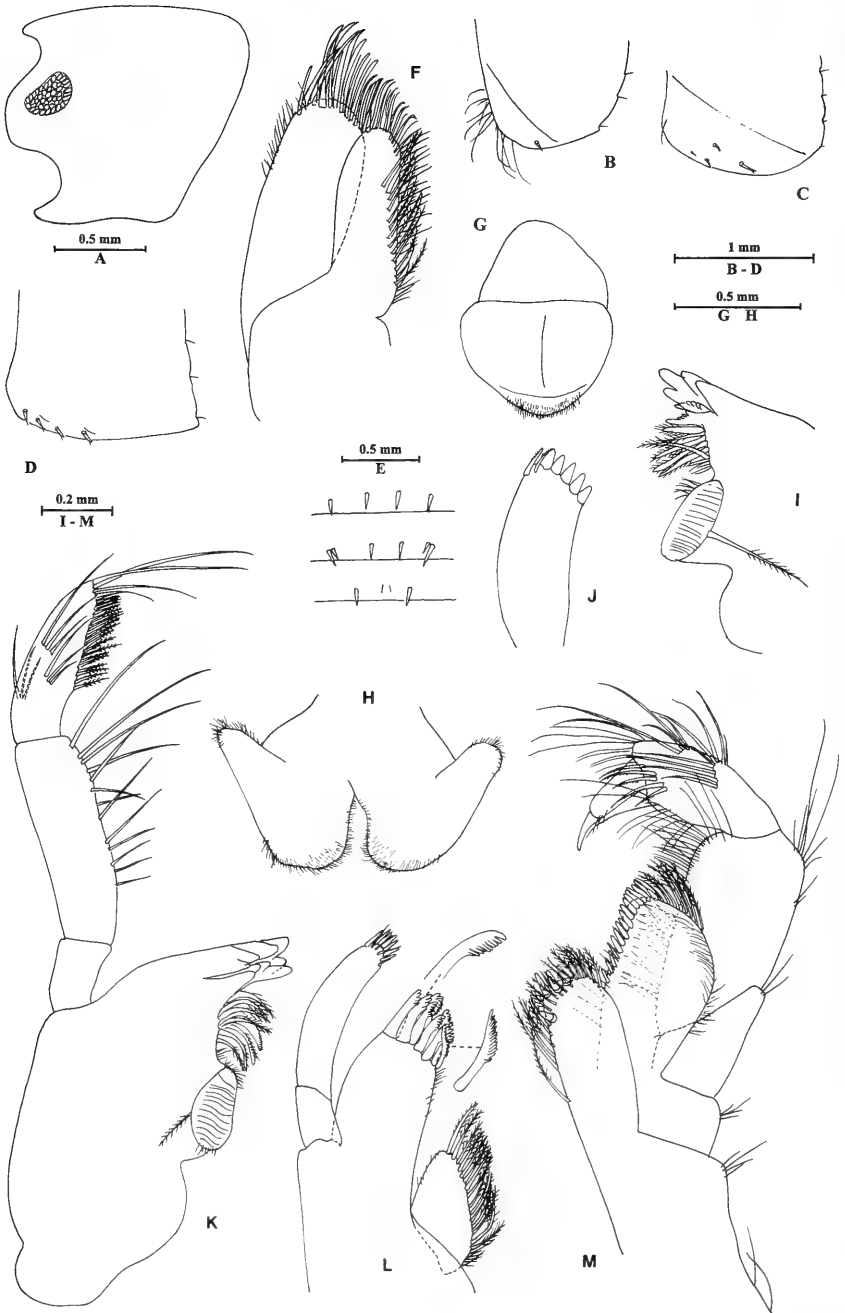


FIG. 1. *Gammarus montanus* sp. n., holotype, male. A, head; B, epimeral plate 1; C, epimeral plate 2; D, epimeral plate 3; E, urosomites (dorsal view); F, maxilla 2; G, upper lip; H, lower lip; I, right mandible; J, palp of right maxilla 1; K, left mandible; L, left maxilla 1; M, maxilliped.

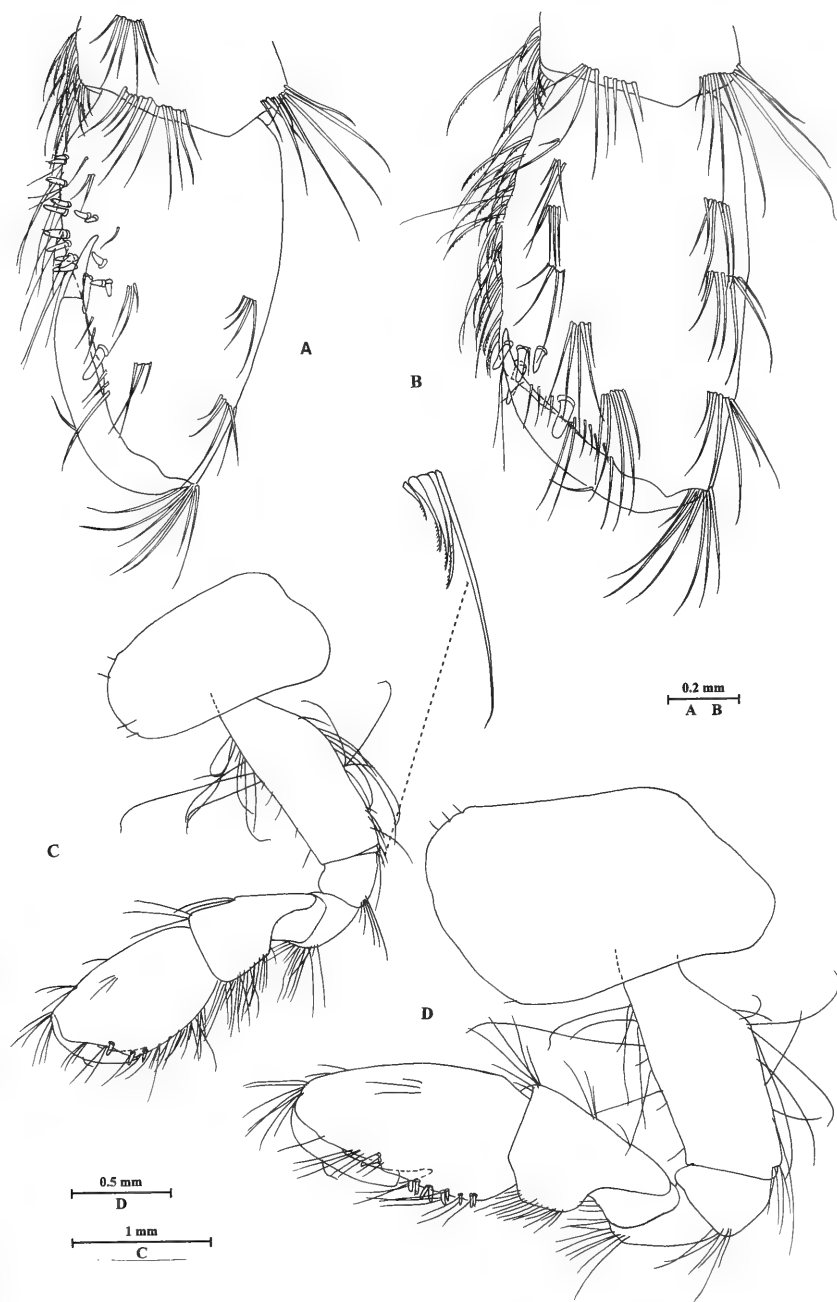


FIG. 2. *Gammarus montanus* sp. n. holotype, male. A, propodus and dactylus of gnathopod 1; B, propodus and dactylus of gnathopod 2; C, gnathopod 2; D, gnathopod 1.

Coxal plates: coxal plates 1-3 subrectangular (Figs 2C, D, 3E), bearing two to three setules on anterior corner and one setule on posterior corner; coxal plate 4 excavate (Fig. 3A), bearing two setules on anterior corner and six setules on posterior margin; anterior lobe of coxal plates 5 and 6 small (Figs 3B, C), posterior lobe with two setules on posterodistal corners; coxal plate 7 (Fig. 3D) with six setules on posterior margin.

Coxal gills: coxal gills present on pereopods 2-7, sac-like.

Gnathopod 1 (Figs 2A, D): basis with long naked setae along lateroproximal and medial margins, four plumose setae on posterodistal corner; carpus reaching 73% length of propodus, bearing two groups of long setae on lateral margin, and a row of long slender setae on medial margin; palm of propodus strongly oblique, bearing one palmar medial robust seta, ten robust setae on lateral margin and six robust setae on medial surface, associated with groups of long naked setae on medial surface; dactylus with one long naked seta on lateral margin.

Gnathopod 2 (Figs 2B, C) larger than gnathopod 1, basis similar to that of gnathopod 1; carpus reaching 75% length of propodus, bearing one group of long naked setae on lateral margin and a row of long setae on medial margin; propodus subrectangular, bearing one blunt palmar medial robust seta, two robust setae on medial posterodistal corner and two robust setae on lateral posterodistal corner, with eight groups of long setae on medial surface; dactylus with one naked seta on lateral margin.

Pereopod 3 (Figs 3E, F) longer than pereopod 4, basis with fourteen slender setae on medial margin, three groups of long setae and three groups of short setae on lateral margin; merus to propodus densely with long setae on medial margins; carpus and propodus accompanied by small robust setae; dactylus with one plumose seta on lateral margin and two stiff setae at hinge of nail.

Pereopod 4 (Figs 3A, G): subequal to pereopod 3, medial margins of merus and carpus with less long straight setae than pereopod 3.

Pereopod 5 (Figs 3B, H): basis nearly straight on medial margin, bearing four short robust seta on lateral margin and a row of eight setules on medial margin; merus bearing three groups of slender setae on lateral margin; carpus with two and three groups of short robust seta along medial and lateral margins; dactylus with 1 plumose seta on lateral margin.

Pereopod 6 (Figs 3C, I): basis weakly concave posteriorly, bearing a group of posterodistal setae on medial surface; merus to propodus bearing two or three groups of robust setae on lateral margins; dactylus with one seta on lateral margin and one stiff seta at hinge of nail.

Pereopod 7 (Figs 3D, J): similar to pereopod 6, basis weakly expanded posteriorly, with one group of posterodistal setae on medial surface.

Epimeral plates: epimeral plates 1-3 bearing three to four short setules on medial margins. Epimeral plate 1 (Fig. 1B) with thirteen long setae on anteroventral corner and one robust seta on medial-ventral margin; epimeral plates 2 and 3 slightly pointed on posterodistal corners (Figs 1C, D), with three robust setae and two setae on ventral margin of plate 2 and four robust setae on ventral margin of plate 3.

Pleopods: pleopods 1-3 subequal in length (Figs 4F-H), peduncle bearing two retinacula accompanied by two setae on anterodistal corner and some long setae on

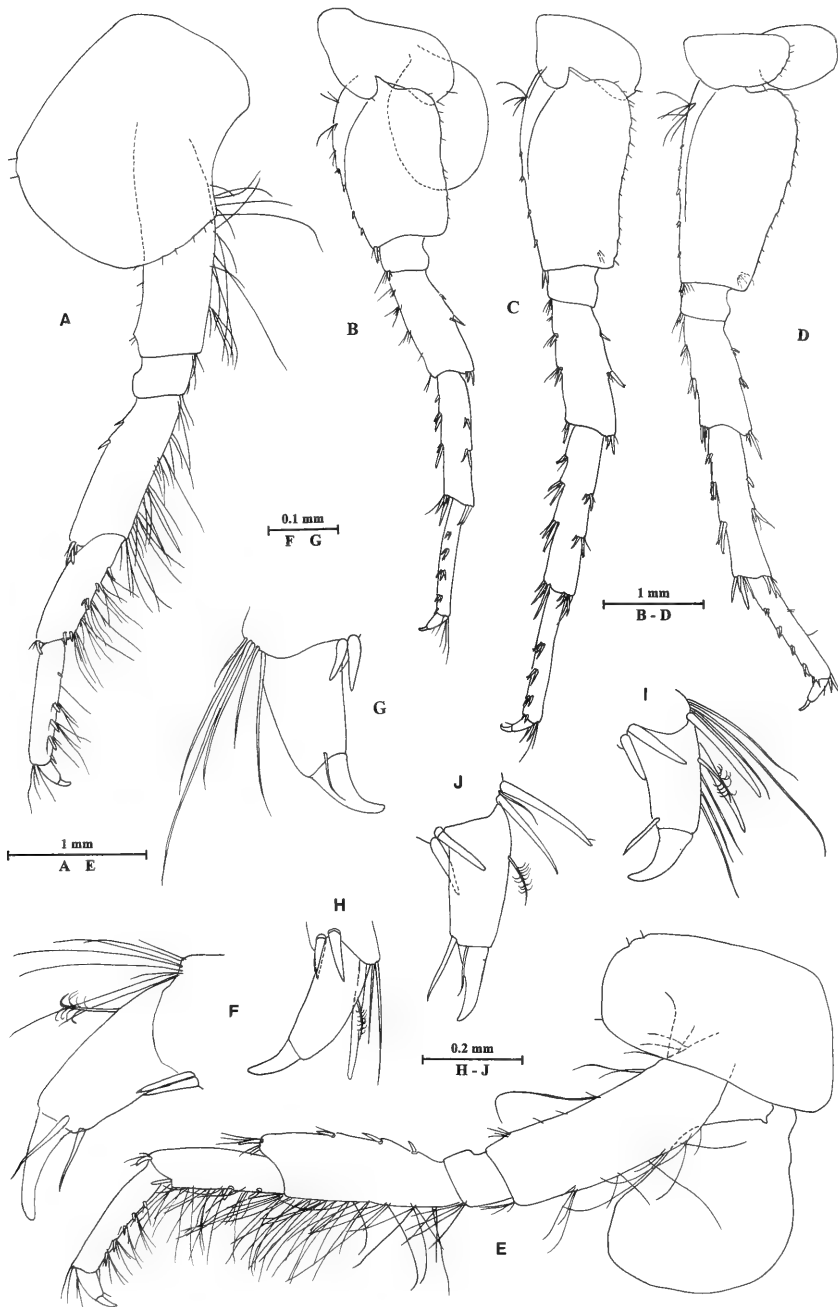


FIG. 3. *Gammarus montanus* sp. n., holotype, male. A, pereopod 4; B, pereopod 5; C, pereopod 6; D, pereopod 7; E, pereopod 3; F, dactylus of pereopod 3; G, dactylus of pereopod 4; H, dactylus of pereopod 5; I, dactylus of pereopod 6; J, dactylus of pereopod 7.

medial surface; both rami thirteen to eighteen articulate, armed with long plumose setae.

Urosomites: urosomites 1-3 without humps dorsally (Fig. 1E), urosomites 1-2 bearing four groups of one or two robust setae accompanied by fine setae on postero-dorsal margins; urosomite 3 with two single robust setae and two single fine setae on posterodorsal margin.

Uropod 1 (Fig. 4E): peduncle with one basofacial robust seta, three robust setae on lateral margin, one robust seta on medial margin, two robust setae on laterodistal corner and one robust seta on mediodistal corner; outer ramus with two robust setae on medial margin and two robust setae on lateral margin; inner ramus with one robust seta on lateral margin and two robust setae on medial margin; both rami with five apical robust setae.

Uropod 2 (Fig. 4D): peduncle longer than both rami, bearing three slender robust setae on lateral margin, one robust seta on medial margin and one distal robust seta on medial and lateral corners; outer ramus a little shorter than inner ramus, bearing one robust seta on medial margin and one robust seta on lateral margin; inner ramus bearing two robust setae on medial margin and one robust seta on lateral margin; both rami bearing five apical robust setae.

Uropod 3 (Fig. 4I): peduncle short, bearing a pair of submarginal robust setae mid-laterally, one robust seta apico-laterally, two robust setae apico-medially, and two robust setae and a seta on the mid-ventrodistal margin; inner ramus short, about 47% length of outer ramus, bearing medially ten long simple setae, without lateral setae, the apex bearing one robust seta accompanied by five long setae; outer ramus two articulate, the second article tiny, about one twentieth the length of the first, and subequal to the three robust apical setae of that article, the second article bearing four long apical setae; the medial margin of the first article with groups of long simple setae, the lateral margin with four robust setae associated with many long simple setae.

Telson (Fig. 4C) cleft to basis, each lobe with two or three distal robust setae accompanied by two to four long slender setae, and with two groups of setae on dorsal surface.

Description of female: length 7.5 mm. Propodus of gnathopod 1 ovate (Fig. 5B), palm not oblique as in male, bearing eight robust setae on posterior margin accompanied by many long setae, and seven groups of setae on medial surface; nail of dactylus elongate, bearing one seta on lateral margin. Propodus of gnathopod 2 subrectangular (Fig. 5A), bearing two robust setae on posteromedial corner and two robust setae on posterolateral corner. Uropod 3 similar to that of male, inner ramus reaching 45% length of article 1 of outer ramus, both rami armed with long simple setae (Fig. 5C). Telson cleft to the basis (Fig. 5E), each lobe with three distal robust setae and one basolateral robust seta. Oostegites of pereopods 2-5 present (Fig. 5D).

Remarks: *Gammarus montanus* sp. n. bears characters in common with *G. gregoryi* Tattersall, 1924 and *G. paucispinus* Hou & Li, 2002b particularly in the presence of simple setae on both margins of uropod 3, and in the shape of the epimeral plates 1-3. *G. montanus* sp. n. can be distinguished from *G. gregoryi* by the absence of calceoli and the inner ramus of uropod 3 which is about half as long as article 1 of the

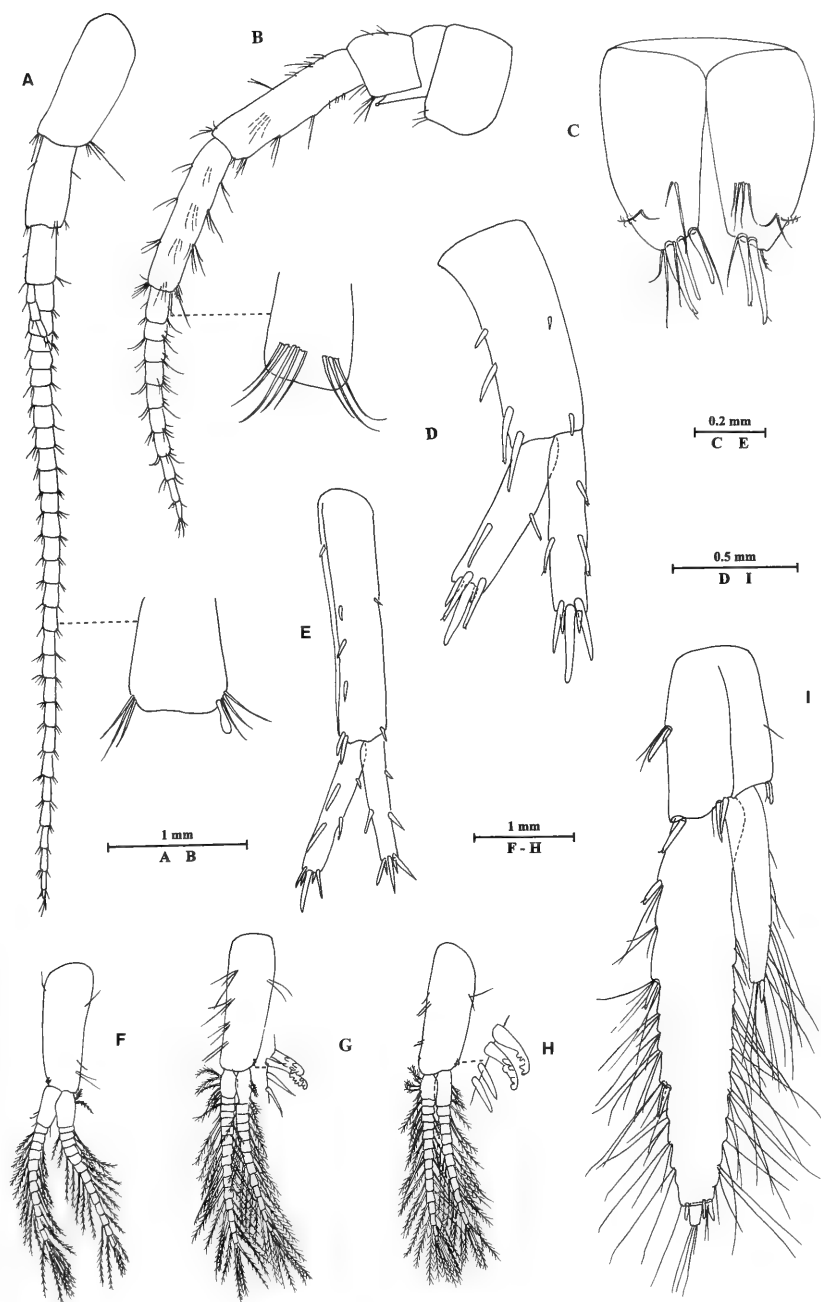


FIG. 4. *Gammarus montanus* sp. n., holotype, male. A, antenna 1; B, antenna 2; C, telson; D, uropod 2; E, uropod 1; F, pleopod 1; G, pleopod 2; H, pleopod 3; I, uropod 3.

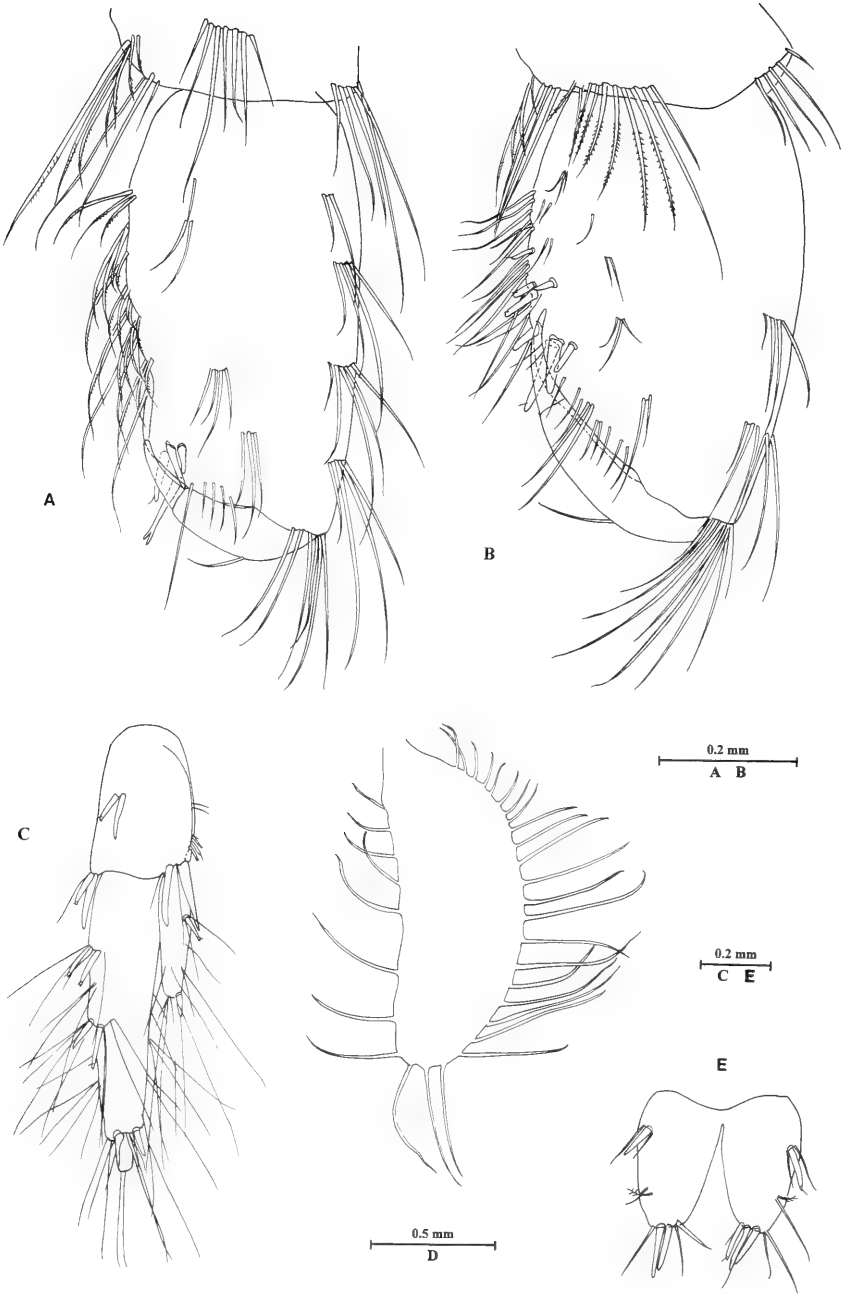


FIG. 5. *Gammarus montanus* sp. n., female. A, propodus and dactylus of gnathopod 2; B, propodus and dactylus of gnathopod 1; C, uropod 3; D, oostegite 2; E, telson.

outer ramus (about one-third in *G. gregoryi*). *G. montanus* sp. n. differs from *G. paucispinus* in that urosomite 1 bears four singly arranged robust setae on the dorsal margin (urosomite 1 only with a few setae in *G. paucispinus*), and the telson bears few long setae on the dorsal margin (telson with groups of long setae on dorsal margin in *G. paucispinus*).

***Gammarus brevipodus* sp. n.**

Figs 6-10

Material: holotype, male (IZCAS-I-A0055), from a feeder stream of the Ili River at the crossroad of National Highway 217 and 218, Xinyuan County (43.25°N, 83.16°E), collected by Dr Zhixiao Liu and Mr Ayiheng, August 16, 2001. Paratypes: 14 males and 5 females (IZCAS), same data as for the holotype; 10 males and 10 females (MHNG), Kunes River, Narat Town (43.2°N, 84.6°E), Xinyuan County, collected by Dr Zhixiao Liu and Mr Ayiheng, August 15, 2001.

Other material: 20 males, 9 females and 15 juveniles, Kunes River, Narat Town, collected by Dr Zhixiao Liu and Mr Ayiheng; August 15, 2001. 25 males, 10 females and 2 juveniles, Bayanbulak (43.0°N, 84.1°E), collected by Dr Zhixiao Liu and Mr Meng Kaibayier, August 17, 2001.

Etymology: the epithet "*brevipodus*" refers to the short inner ramus of uropod 3.

Diagnosis: *Gammarus brevipodus* sp. n. belongs to the *G. balcanicus*-group. *Gammarus brevipodus* sp. n. can be distinguished by the following characters: (1) antenna 2 with long setae along both margins, (2) calceoli absent, (3) uropod 3 armed with few setae, (4) article 2 of outer ramus in uropod 3 subequal to adjacent robust setae.

Description of male: body length 14.5 mm.

Head (Fig. 6A): lateral cephalic lobe truncate, inferior antennal sinus deep, eyes relatively small.

Antenna 1 (Fig. 9F): peduncular articles 1-3 in length ratio 1 : 0.7 : 0.44, bearing short distal setae; primary flagellum twenty articulate, most articles with aesthetascs; accessory flagellum four articulate.

Antenna 2 (Fig. 9E): peduncular article 4 a little shorter than article 5, both articles with long setae along anterior and posterior margins; flagellum eight articulate, with some distal short setae, calceoli lacking.

Upper lip convex (Fig. 6D), with minute setules.

Mandibles (Figs 6H, I): left incisor with five teeth; lacinia mobilis with four dentitions; molar triturative, bearing one plumose seta; article 2 of palp with seventeen long stiff setae on medial margin, article 3 reaching 80% length of article 2, bearing two groups of long simple B-setae on medial surface, seven long simple A-setae on lateral surface, a row of D-setae on medial margin and four E-setae. Right incisor with four teeth, lacinia mobilis bifurcate, with several weak teeth at ridge.

Lower lip (Fig. 6C): inner lobe absent.

Maxilla 1 (Figs 6F, G): inner plate triangular, medial margin bearing several slender setules basally, and twelve plumose setae evenly distributed between the base and apex; outer plate subrectangular, sparsely setose medially, the apex bearing eleven serrate robust setae; palp 2 articulate, the left second article weakly falcate, bearing mediodistally a single short stout seta, apically 4 robust naked setae and three stiff setules apico-facilly; the right second article bearing five broad-based tooth setae and two stiff slender setae.

Maxilla 2 (Fig. 6E): inner plate with an oblique row of ten plumose setae on the medial surface, evenly distributed between the base and apex; the outer plate bearing slender setae apically.

Maxilliped (Fig. 6J): inner plate bearing one subapical and three apical robust tooth setae, associated with plumose setae on medial and apical margins; outer plate bearing thirteen blade-like robust setae on medial margin and 6 apical pectinate setae; palp 4 articulate.

Coxal plates: coxal plates 1-3 subrectangular (Figs 7A, B, 8A), with three to five short setules on anteroventral corner and one seta on posteroventral corner; coxal plate 4 excavate (Fig. 8B), with four setules on anteroventral corner, 8 setules on medial margin and some minute facial setae; anterior lobe of coxal plates 5 and 6 small (Figs 8C, D), with one or two setules on anteroventral corner, posterior margin with three or two setules; coxal plate 7 (Fig. 9A) with five setules on medial margin.

Gnathopod 1 (Figs 7A, C): basis with long setae on lateroproximal and medial margin, with four plumose setae on posterodistal corner accompanied by three long setae; carpus reaching 75% length of propodus, bearing one group of long setae on lateral margin and several groups of setae on medial margin; propodus pyriform, palm oblique, bearing one medial stout robust seta, ten robust setae on lateral margin and six robust setae on medial surface, associated with groups of long setae on medial surface; dactylus with 1 seta on lateral margin.

Gnathopod 2 (Figs 7B, D): basis similar to that of gnathopod 1; carpus reaching 86% length of propodus, with subparallel margins; propodus subrectangular, palm with one medial stout robust seta, four robust setae on lateral posterodistal corner, two robust setae on medial posterodistal corner, and seven groups of long setae on medial surface; dactylus with one seta on lateral margin.

Pereopod 3 (Figs 8A, E) slender, basis with four long setae on lateral margin and fifteen setae on medial margin; merus with two single robust setae on lateral margin and three groups of short setae on medial margin; carpus with three short robust setae accompanied by short setae on medial margin; propodus with four groups of short robust setae on medial margin; dactylus with one seta on lateral margin and two stiff setae at hinge of nail.

Pereopod 4 (Figs 8B, F): armature similar to that of pereopod 3.

Pereopod 5 (Figs 8C, G): basis nearly straight on medial margin, with five single robust setae on lateral margin and a row of twenty short setae on medial margin; merus with two groups of short setae on lateral margin; carpus with two groups of short robust setae on lateral and medial margins; propodus with four groups of short robust setae on lateral margin and a few short setae on medial margin; dactylus with one plumose seta on lateral margin and 2 setae at hinge of nail.

Pereopod 6 (Figs 8D, H): similar to pereopod 5, basis weakly concave on medial margin, lateral margins of merus to propodus with two to four groups of robust setae and fine setae.

Pereopod 7 (Figs 9A, G): basis weakly expanded on medial margin, medial surface with one robust seta on posterodistal corner.

Epimeral plates: epimeral plates 1-3 with five to six short setules on postero-medial margins. Epimeral plate 1 ventrally rounded (Fig. 6L), with seven setae on

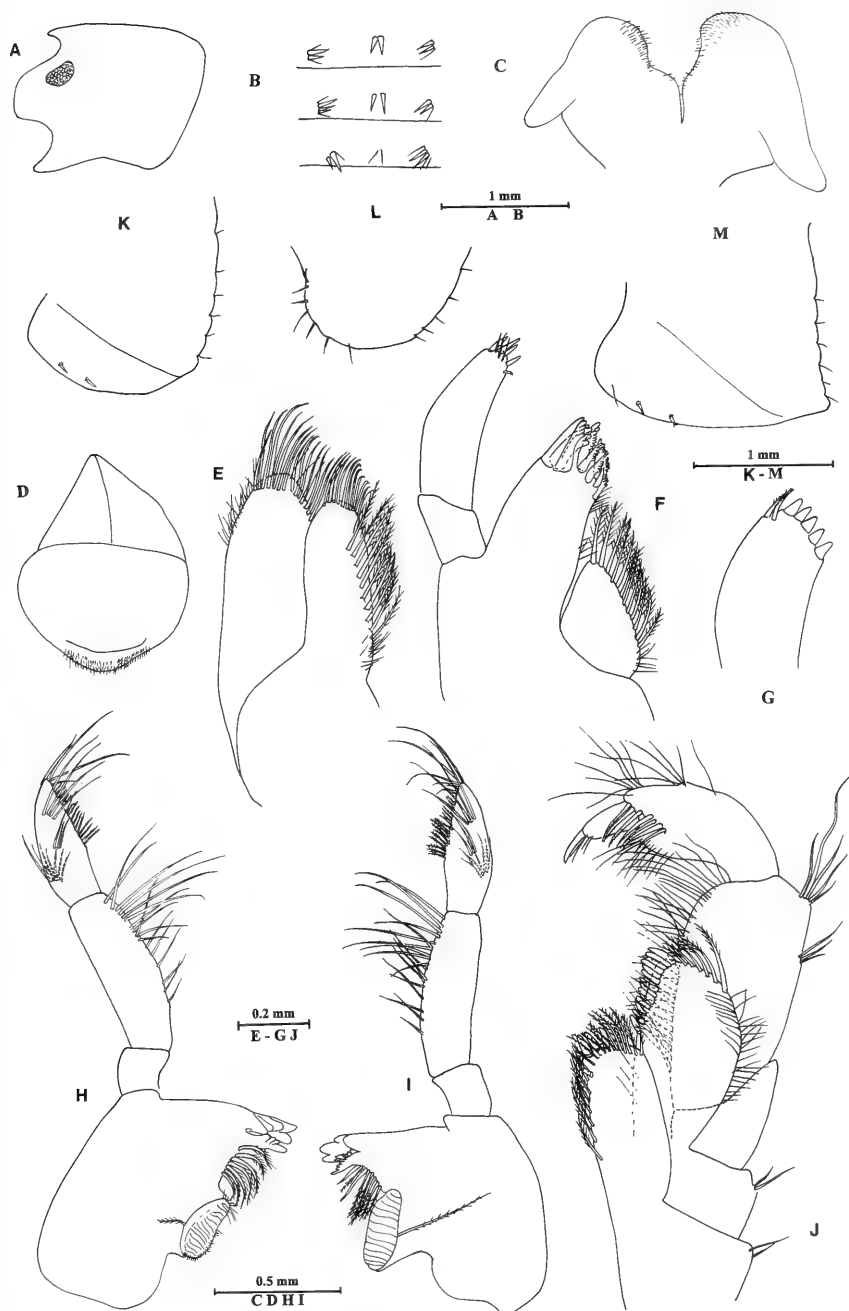


FIG. 6. *Gammarus brevipodus* sp. n., holotype, male. A, Head; B, urosomites (dorsal view); C, lower lip; D, upper lip; E, maxilla 2; F, left maxilla 1; G, palp of right maxilla 1; H, left mandible; I, right mandible; J, maxilliped; K, epimeral plate 2; L, epimeral plate 1; M, epimeral plate 3.

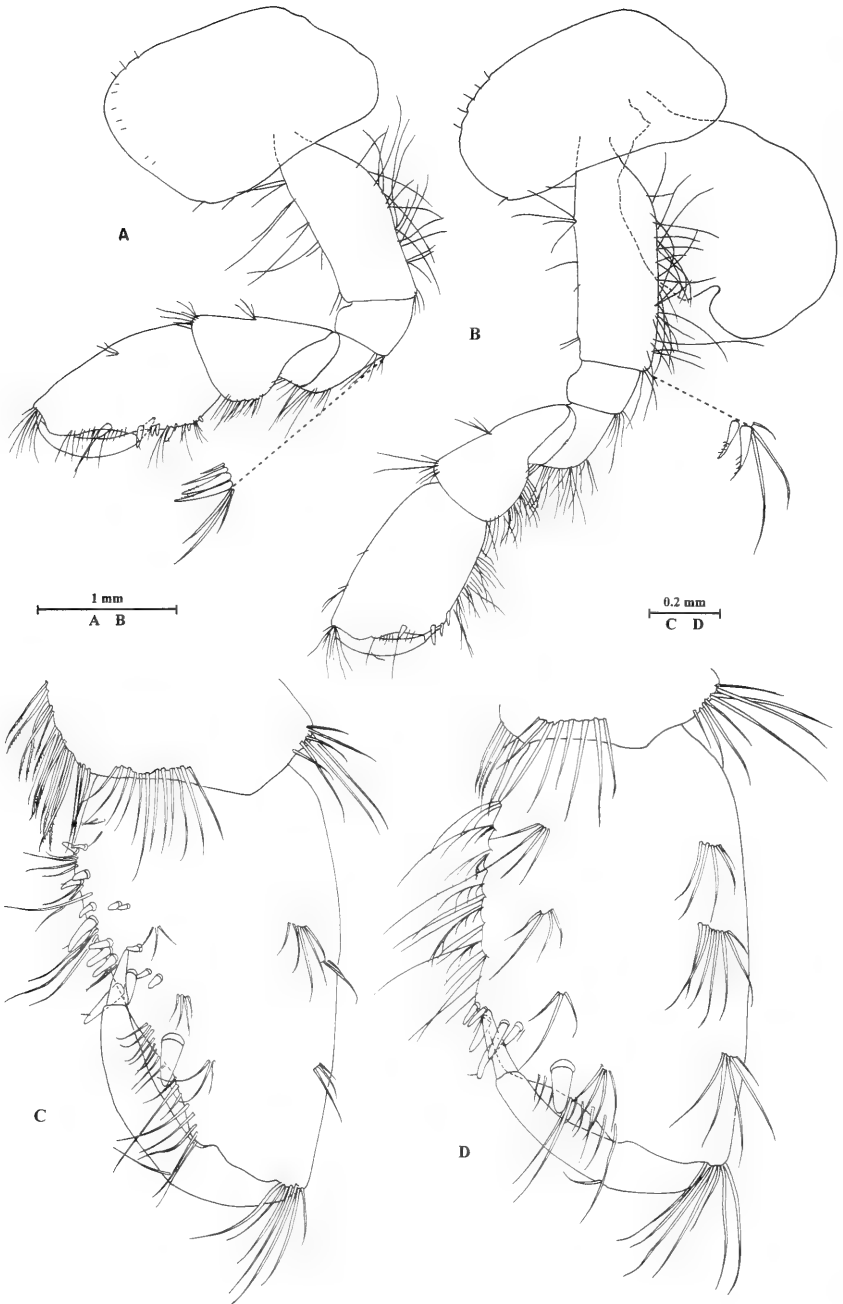


FIG. 7. *Gammarus brevipodus* sp. n., holotype, male. A, gnathopod 1; B, gnathopod 2; C, propodus and dactylus of gnathopod 1; D, propodus and dactylus of gnathopod 2.

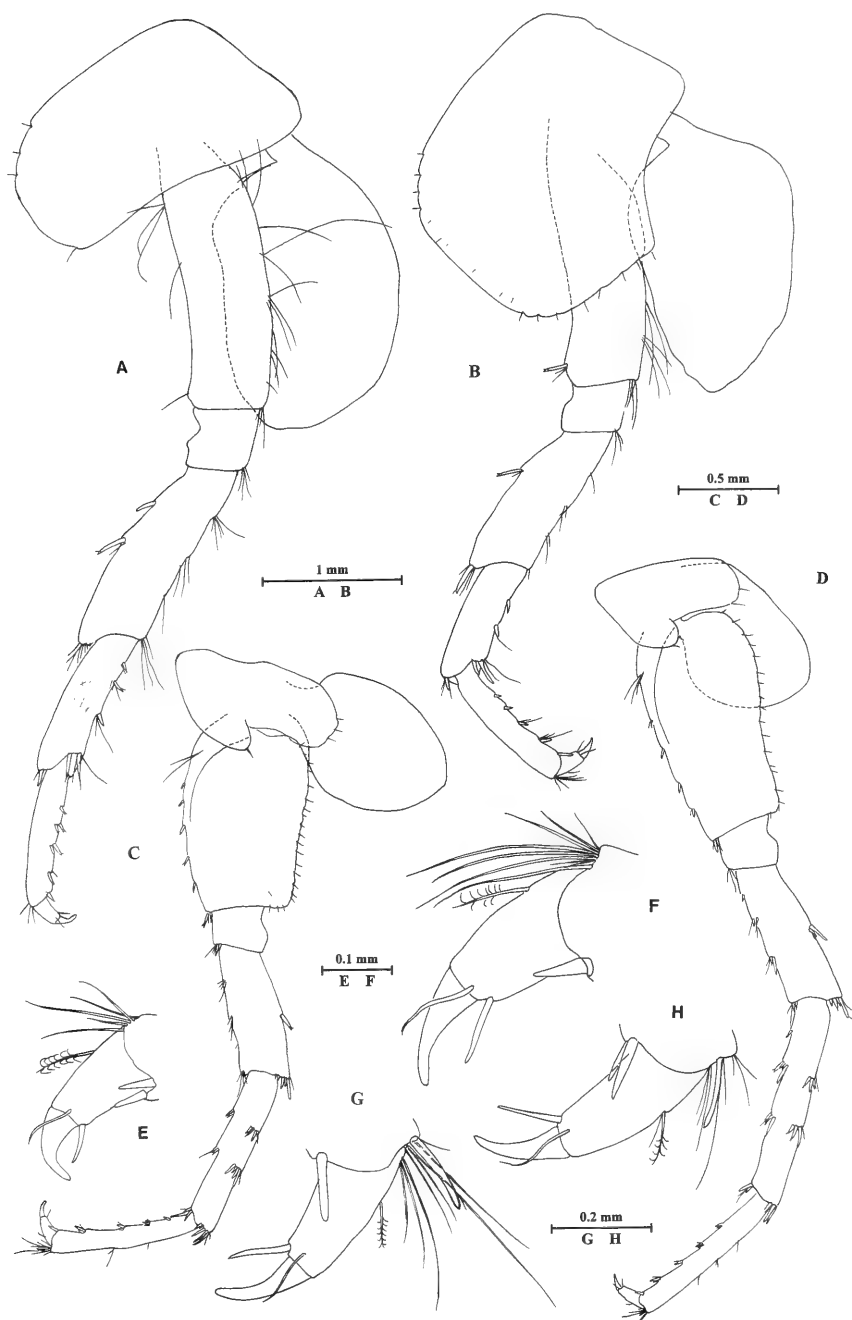


FIG. 8. *Gammarus brevipodus* sp. n., holotype, male. A, pereopod 3; B, pereopod 4; C, pereopod 5; D, pereopod 6; E, dactylus of pereopod 3; F, dactylus of pereopod 4; G, dactylus of pereopod 5; H, dactylus of pereopod 6.

anterior corner; epimeral plate 2 with blunt posterior corner (Fig. 6K), bearing two ventrofacial robust setae; epimeral plate 3 with weakly pointed posterodistal corner (Fig. 6M), bearing one seta and two robust setae on ventrofacial margin.

Pleopods: pleopods 1-3 subequal in length (Figs 9H-J), peduncle with two retinacula accompanied by two setae on anterodistal corners; both rami subequal, twelve to eighteen articulate, armed with long plumose setae.

Urosomites: urosomites 1-3 without humps dorsally, urosomites 1-2 with three groups of robust setae accompanied by fine setae on posterodorsal margins; urosomite 3 with two pairs of robust setae accompanied by fine setae and two fine medial setules on posterodorsal margin (Fig. 6B).

Uropod 1 (Fig. 9L): peduncle longer than rami, with one basofacial robust seta, three robust setae on lateral margin, three robust setae on medial margin, two robust setae on laterodistal corner and one mediobasal robust seta; inner ramus with two robust setae on medial margin and one robust seta on lateral margin; outer ramus with two robust setae on lateral margin and one robust seta on medial margin; both rami with five distal robust setae.

Uropod 2 (Fig. 9K): peduncle longer than both rami, bearing two robust setae on lateral margin, one robust seta on medial margin, and one robust seta on laterodistal and mediobasal corners; outer ramus with one robust seta on lateral margin; inner ramus with one robust seta on lateral margin and one robust seta on medial margin.

Uropod 3 (Fig. 10A): peduncle short, bearing a pair of submarginal short robust setae mid-laterally, two robust setae apico-laterally, three robust setae apico-medially, and a pair of slender setules and a single robust seta on the mid-ventrodorsal margin; inner ramus short, about one third the length of the outer ramus, bearing medially two robust setae, each with an associated fine seta, and a single small seta distally, without lateral setae, the apex bearing two robust setae, one long and two short fine setae; the outer ramus two articulate, the second article tiny, about one fifteenth the length of the first, and subequal to the six robust apical setae of that article, the second article bearing three fine apical setae; the medial margin of the first article with five transverse rows of mixed robust and fine setae, the lateral margin with five rows.

Telson (Fig. 9B) cleft 75%, each lobe with three robust setae and two or three slender setae on the distal margin of each lobe, only a single facial setule on the left lobe.

Description of female: body length 13.8 mm. Gnathopod 1: coxal plate with four setae on anterior corner and three setae on posterior corner; propodus not oblique as in male, with six robust setae on posterior corner (Fig. 10C). Gnathopod 2: carpus about as long as propodus, propodus subrectangular, with one robust seta on posterior corner, nail of dactylus elongate (Fig. 10D). Bases of pereopods 5-7 similar to those of male (Figs 10E-G). Uropod 3 (Fig. 10B): inner ramus less than 30% length of article 1 of outer ramus. Oostegites present on pereopods 2-5 (Fig. 10G).

Remarks: *Gammarus brevipedus* sp. n. is similar to *G. balcanicus* Schaferna, 1923 in pereopods 3 and 4 with few setae and the shape of epimeral plates. *Gammarus brevipedus* sp. n. differs from *G. balcanicus* by (1) peduncle of antenna 2 with long setae along both margins and calceoli absent, (2) inner ramus of uropod 3 about one-

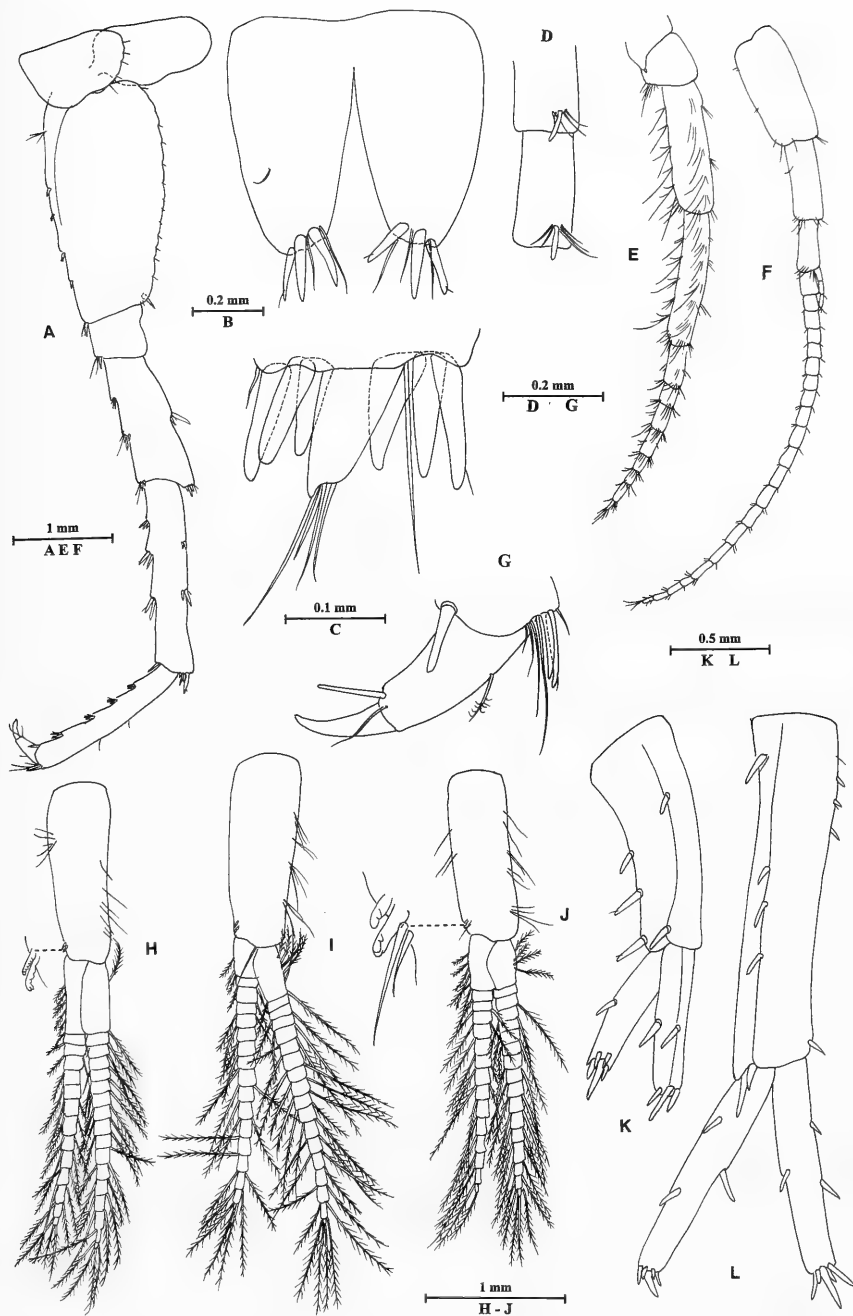


FIG. 9. *Gammarus brevipodus* sp. n., holotype, male. A, pereopod 7; B, telson; C, terminal article of uropod 3; D, flagellum of antenna 1; E, antenna 2; F, antenna 1; G, dactylus of pereopod 7; H, pleopod 1; I, pleopod 2; J, pleopod 3; K, uropod 2; L, uropod 1.

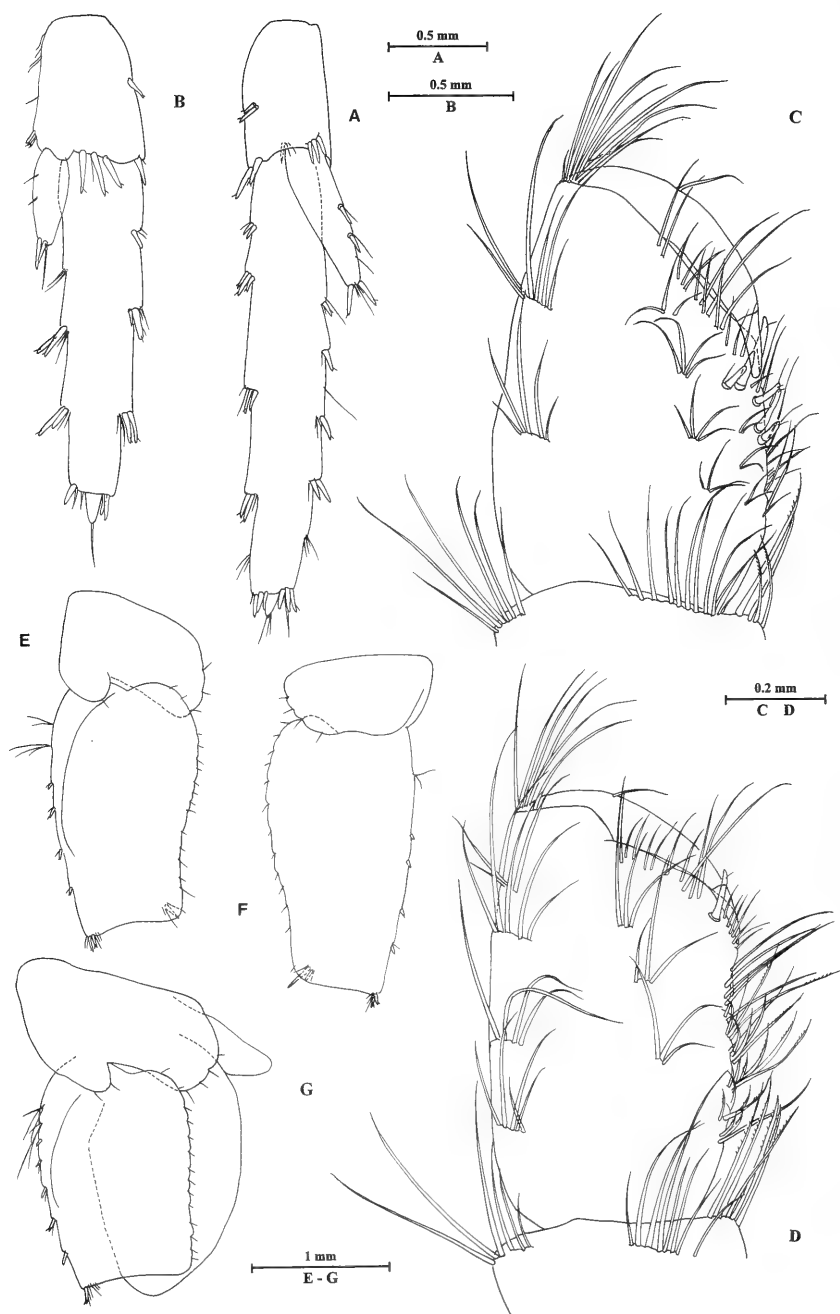


FIG. 10. *Gammarus brevipodus* sp. n., male: A, female: B - G. A, uropod 3; B, uropod 3; C, propodus and dactylus of gnathopod 1; D, propodus and dactylus of gnathopod 2; E, basis of pereopod 6; F, basis of pereopod 7; G, basis of pereopod 5.

third of outer ramus, article 2 of outer ramus of uropod 3 very short, and both rami with few setae in both margins, (3) telson with very few setae on dorsal margin. *G. brevipedus* sp. n. differs from *G. montanus* by pereopods 3 and 4 and uropod 3 with few long setae.

Gammarus takesensis sp. n.

Figs 11-15

Material: holotype, male (IZCAS-I-A0057), Takes River (a feeder stream of the Ili River) near Takes County (43.13°N, 81.49°E), collected by Dr Zhixiao Liu and Mr Ayiheng, August 11, 2001. Paratypes: 20 males and 10 females (IZCAS), 9 males and 9 females (MHNG), same data as for the holotype.

Etymology: the specific name refers to the county of origin.

Diagnosis: *Gammarus takesensis* sp. n. belongs to the *G. balcanicus*-group and is characterized by: peduncle of antenna 2 with a few long setae, article 2 of outer ramus of uropod 3 elongate, medial margin of outer ramus and both margins of inner ramus of uropod 3 with short plumose setae, respectively.

Description of male: body length 12.5 mm.

Head: inferior antennal sinus deep, eyes medium in size (Fig. 11A).

Antenna 1 (Figs 14B, C): peduncular articles 1-3 in length ratio 1 : 0.65 : 0.37, with some distal fine setae; primary flagellum twenty-eight articulate, most articles with aesthetascs; accessory flagellum four articulate.

Antenna 2 (Figs 14A, D): peduncular article 4 about as long as article 5, both with some short setae along anterior and posterior margins; flagellum twelve articulate, bearing short setae, some articles with calceoli.

Upper lip (Fig. 11C) convex, with minute setules apically.

Mandibles (Figs 11H, I): left incisor with five teeth; lacinia mobilis with four dentitions; molar triturative; article 2 of palp with thirteen long stiff setae on medial margin, article 3 reaching 75% length of article 2, with six A-setae on lateral surface and five long B-setae on medial surface, a row of twenty short plumose D-setae and five long E-setae. Incisor of right mandible with four teeth; lacinia mobilis bifurcate, with weak teeth at ridge; molar with one long seta.

Lower lip: inner lobe absent (Fig. 11E).

Maxilla 1 (Figs 11F, G): inner plate triangular, medial margin bearing several setules basally, and fourteen plumose setae evenly distributed between the base and apex; outer plate subrectangular, the apex bearing eleven serrate robust setae; palp two articulate, the left second article weakly falcate, bearing apically seven robust naked setae and three stiff setules apico-facially; the right second article apically bearing four blunt robust setae and two stiff setae.

Maxilla 2 (Fig. 11D): inner plate bearing a row of thirteen plumose setae on medial surface, evenly distributed between the base and apex; outer plate bearing long stiff setae apically and fine pubescence on lateral margin.

Maxilliped (Fig. 11J): inner plate with one subapical robust seta and three blunt apical robust setae, associated with plumose setae on medial and apical margins; outer plate with seven slender robust setae on medial margin accompanied by short naked setae on medial margin and six pectinate setae apically; palp four articulate.

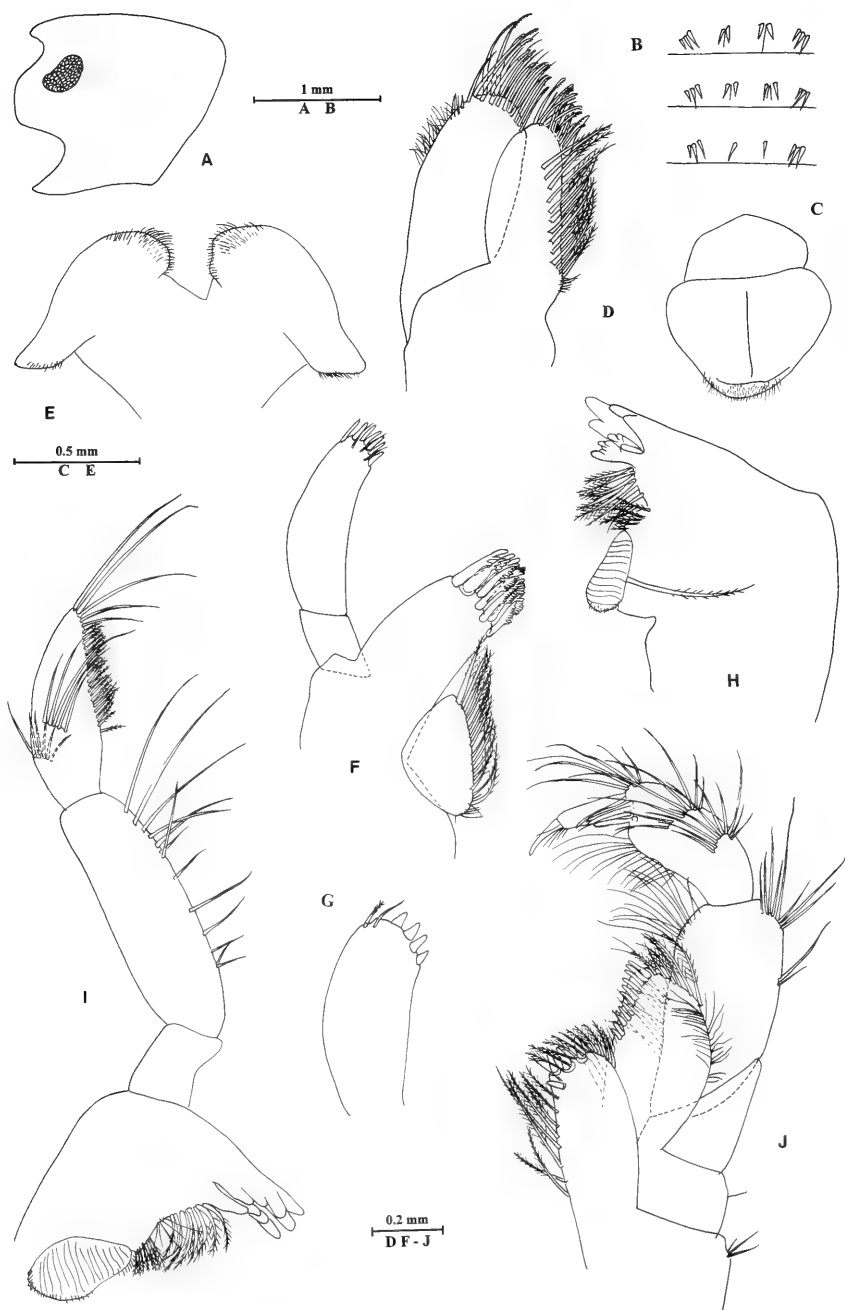


FIG. 11. *Gammarus takesensis* sp. n., holotype, male. A, head; B, urosomites (dorsal view); C, upper lip; D, maxilla 2; E, lower lip; F, left maxilla 1; G, palp of right maxilla 1; H, right mandible; I, left mandible; J, maxilliped.

Coxal plates: coxal plates 1-3 subrectangular (Figs 12A, B, 13B), with two to four setules on anterior corner and one setule on posterior corner; coxal plate 4 excavate (Fig. 13E), with two setules on anterior corner and six setules on medial margin; anterior lobe of coxal plates 5 and 6 (Figs 13C, D) small, with one setule, posterior lobe with one or two setules; coxal plate 7 shallow (Fig. 13F), with three setules on medial margin.

Gnathopod 1 (Figs. 12A, C): basis stout, bearing long setae on lateroproximal and medial margins; carpus reaching 72% length of propodus; palm of propodus oblique, bearing one palmar medial robust seta, five groups of robust setae on lateral margin, three groups of robust setae on medial surface, associated with five to seven groups of setae on medial surface; nail of dactylus short, bearing one naked seta on lateral margin.

Gnathopod 2 (Figs 12B, D): basis similar to that of gnathopod 1; carpus reaching 80% of propodus, with parallel-sided margins, bearing one group setae on lateral margin and many setae on medial margin; propodus subrectangular, bearing one medial palmar robust seta, two robust setae on medial posterodistal corner, two robust setae on lateral posterodistal corner and seven groups of long setae on medial surface; dactylus with one seta on lateral margin.

Pereopod 3 (Figs 13B, G): basis with four groups of long setae on medial margin; merus with one seta and one robust seta accompanied by one seta on lateral margin, and three groups of setae on medial margin; carpus with two pairs of robust setae accompanied by fine setae on medial margin; propodus with three single robust setae and a pair of robust setae on medial margin; dactylus with one plumose seta on lateral margin and two stiff setae at hinge of nail.

Pereopod 4 (Figs 13E, H): subequal to pereopod 3, merus and carpus with less setae on medial margin.

Pereopod 5 (Figs 13C, I): basis nearly straight on medial margin, bearing four single short robust setae on lateral margin and a row of ten short setules on medial margin; merus bearing two single robust setae accompanied by one fine setule on lateral margin, and one short robust seta on medial margin; carpus with a pair of short robust setae on lateral margin and a group of three short robust setae on medial margin; propodus with three pair of short robust setae on lateral margin; dactylus with one plumose seta on lateral margin and two stiff setae at hinge of nail.

Pereopod 6 (Figs 13D, J): similar to pereopod 5 except for basis weakly concave on posterior margin.

Pereopod 7 (Figs 13F, K): similar to pereopod 5, basis slightly expanded on medial margin, bearing two posterodistal setae on medial surface.

Epimeral plates: epimeral plates 1-3 with two or three short setules on postero-medial margins. Epimeral plate 1 ventrally rounded (Fig. 15D), bearing ten setae on anteroventral corner; epimeral plates 2 and 3 with slightly pointed posterior corners (Figs 15E, F), bearing one to two setae and two to four robust setae on ventral margin.

Pleopods: pleopods 1-3 subequal in length (Figs 14H-J), peduncle with some setae on medial surface, bearing two retinacula accompanied by two setae on anterodistal corner; both rami eighteen to twenty articulate, fringed with plumose setae.

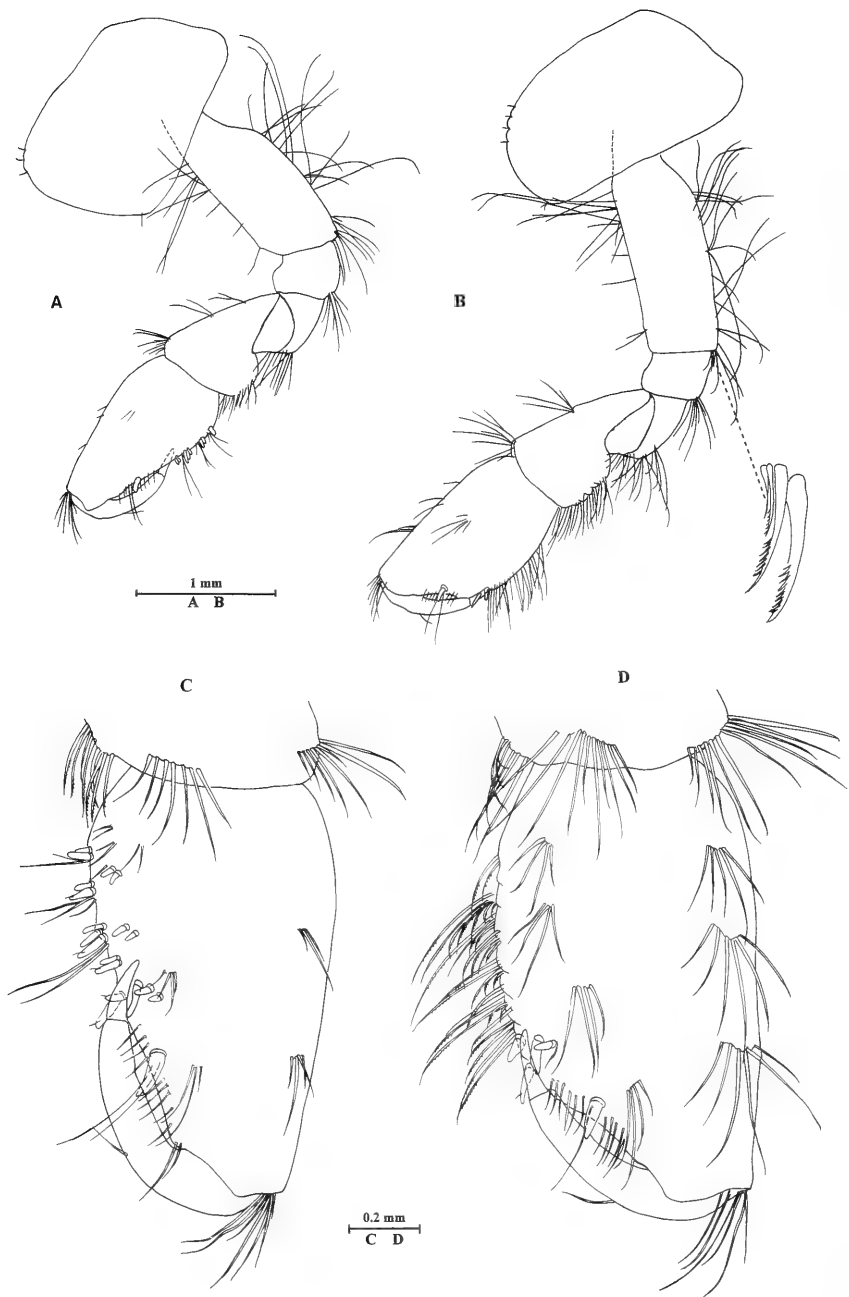


FIG. 12. *Gammarus takesensis* sp. n., holotype, male. A, gnathopod 1; B, gnathopod 2; C, propodus and dactylus of gnathopod 1; D, propodus and dactylus of gnathopod 2.

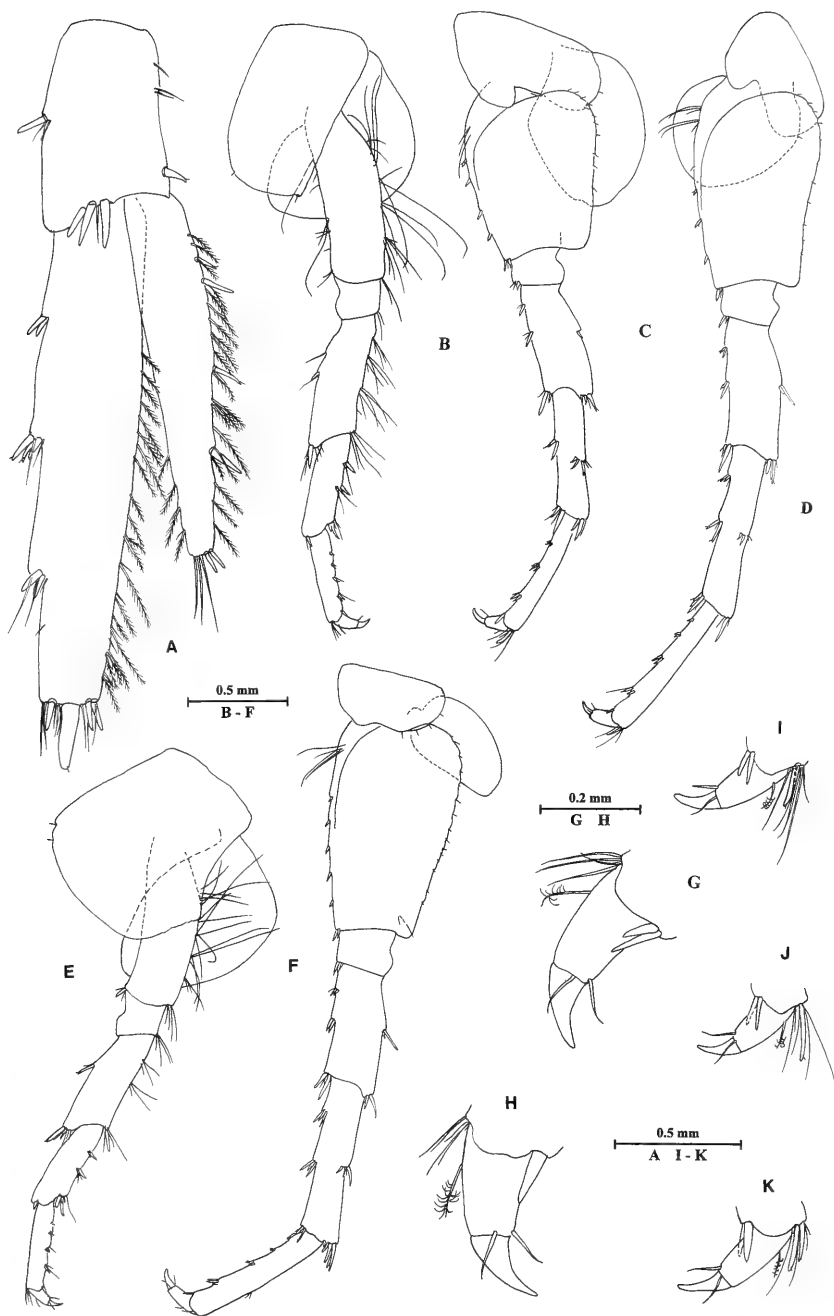


FIG. 13. *Gammarus takesensis* sp. n., holotype, male. A, uropod 3; B, pereopod 3; C, pereopod 5; D, pereopod 6; E, pereopod 4; F, pereopod 7; G, dactylus of pereopod 3; H, dactylus of pereopod 4; I, dactylus of pereopod 5; J, dactylus of pereopod 6; K, dactylus of pereopod 7.

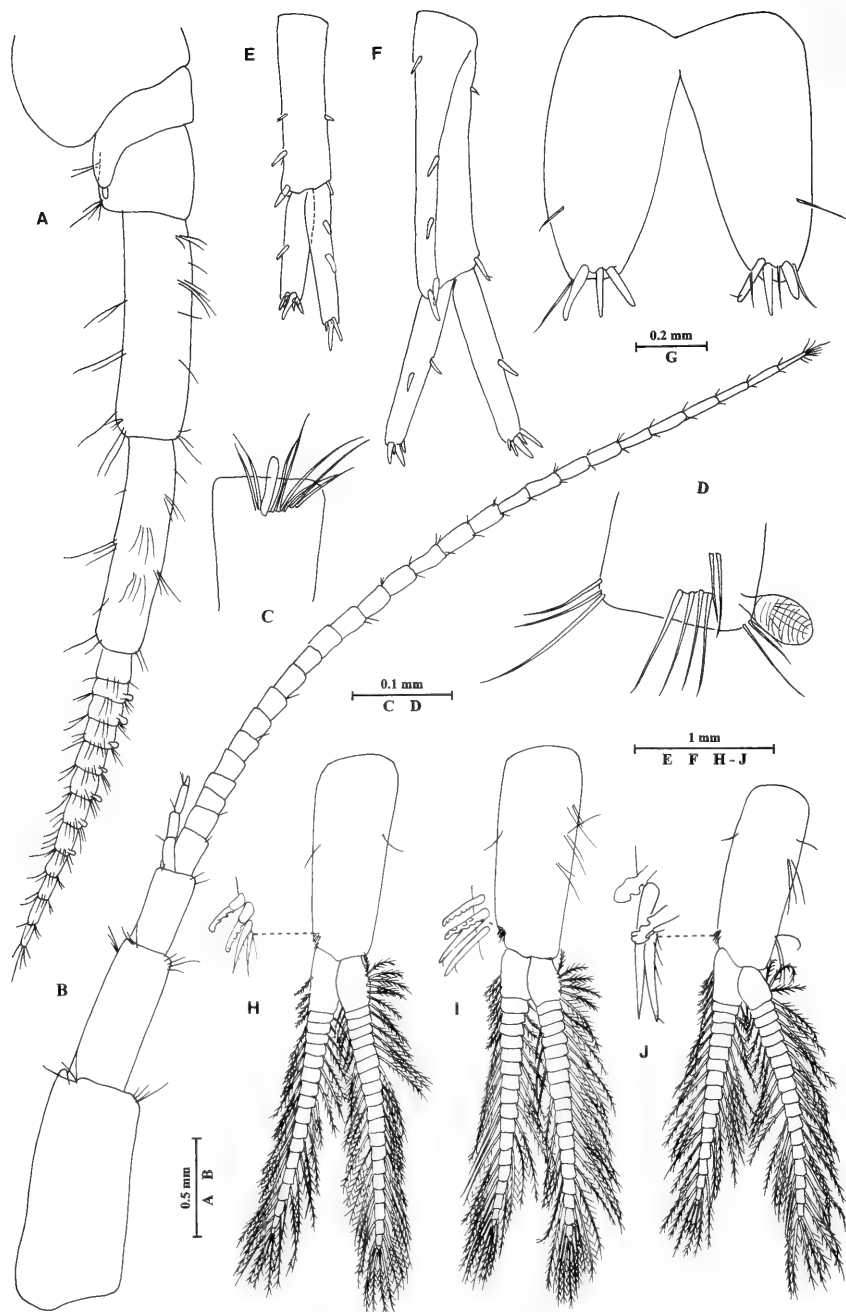


FIG. 14. *Gammarus takesensis* sp. n., holotype, male. A, antenna 2; B, antenna 1; C, flagellum of antenna 1; D, flagellum of antenna 2; E, uropod 2; F, uropod 1; G, telson; H, pleopod 1; I, pleopod 2; J, pleopod 3.

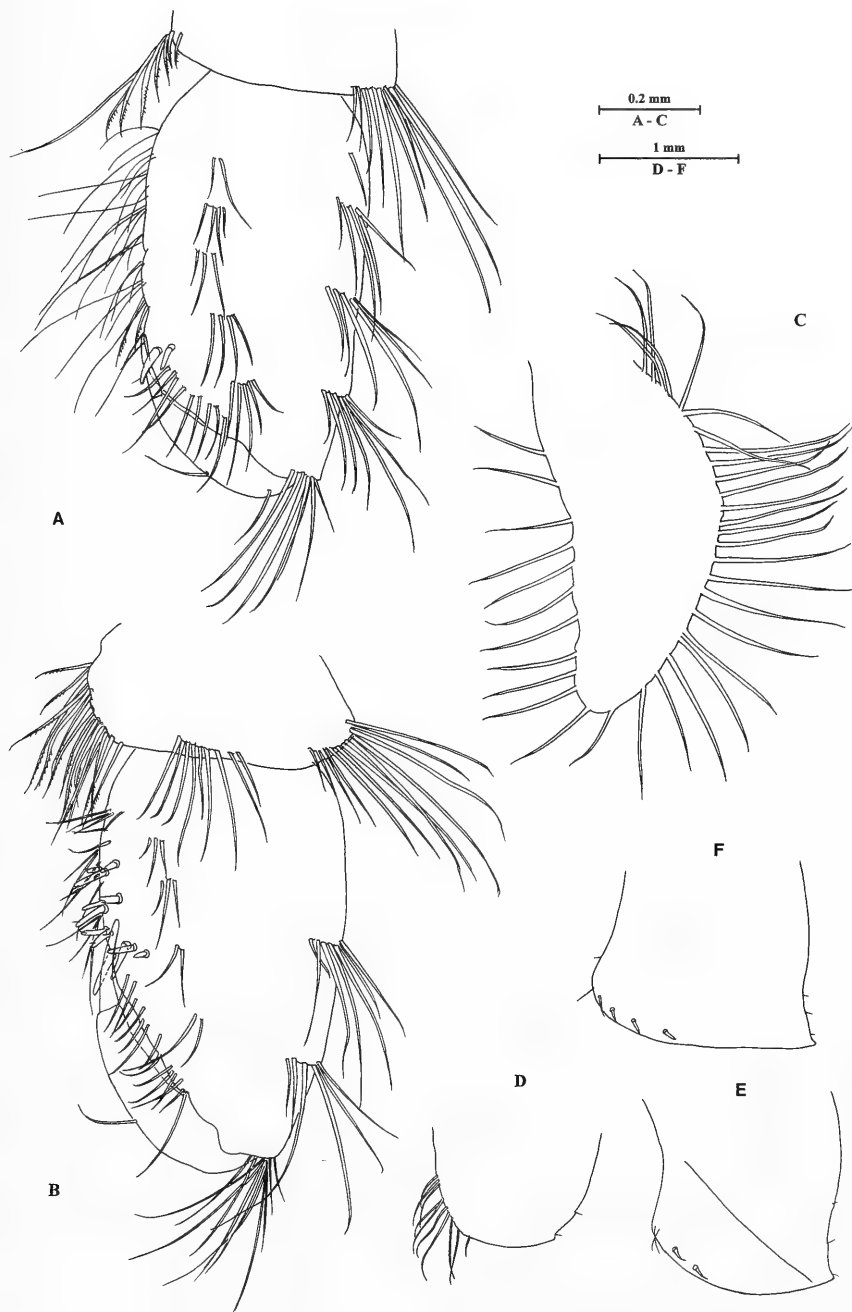


FIG. 15. *Gammarus takesensis* sp. n., female: A – C, male: D – F. A, propodus and dactylus of gnathopod 2; B, propodus and dactylus of gnathopod 1; C, oostegite 2; D, epimeral plate 1; E, epimeral plate 2; F, epimeral plate 3.

Urosomites (Fig. 11B): urosomites 1-3 dorsally flat, bearing four groups of one to three robust setae accompanied by fine setae on posterodorsal margins.

Uropod 1 (Fig. 14F): peduncle longer than both rami, bearing one basofacial robust seta, two robust setae on lateral margin, one short robust seta on medial margin, two robust setae on laterodistal corner and one robust seta on mediiodistal corner; outer ramus with one robust seta on lateral and medial margins; inner ramus with one robust seta on medial margin; both rami with five distal robust setae.

Uropod 2 (Fig. 14E): peduncle longer than both rami, bearing two robust setae on lateral margin, one robust seta on medial margin, and one robust seta on laterodistal and mediiodistal corner; outer ramus shorter than inner ramus, with one robust seta on lateral margin; inner ramus with two robust setae on medial margin; both rami with five distal robust setae.

Uropod 3 (Fig. 13A): peduncle short, bearing a short robust seta mid-laterally, a single robust seta apico-medially, and three robust setae on the mid-ventrodistal margin; inner ramus reaching 74% length of article 1 of outer ramus, bearing medially four robust setae accompanied by a row of short plumose setae, the apex bearing two robust setae and three long naked setae; the outer ramus two articulate, the second article reaching 13% length of first article, and longer than the three robust apical setae of that article, the second article bearing one fine setule apically; the medial margin of the first article with a row of short plumose setae and the lateral margin with three groups of robust setae accompanied by fine setae.

Telson deeply cleft (Fig. 14G), each lobe with three distal robust setae accompanied by one to three long setae, and 1 lateral seta.

Description of female: body length 11.2 mm. Propodus of gnathopod 1 (Fig. 15B) so strongly as in the male, bearing twelve robust setae on medial margin; dactylus with one seta on lateral margin, nail elongate. Propodus of gnathopod 2 with only slightly oblique distal margin (Fig. 15A), bearing two robust setae on medial margin. Oostegites of pereopods 2-5 present.

Remarks: *Gammarus takesensis* sp. n. is similar to *G. brevipodus* sp. n. in the shape of gnathopods 1 and 2, and in the armature of pereopods 3 and 4 and telson. *G. takesensis* sp. n. differs from the latter by the presence of calceoli, inner ramus of uropod 3 reaching three-fourths of outer ramus, article 2 of outer ramus of uropod 3 longer than adjacent robust setae, and medial margin of outer ramus and both margins of inner ramus of uropod 3 with short plumose setae.

G. takesensis sp. n. is also similar to *G. bosniacus* Schaferna, 1923 in pereopods 3 and 4 with few setae, and uropod 3 with some short plumose setae in medial margin of outer ramus. *G. takesensis* sp. n. differs from the latter by accessory flagellum of antenna 1 with four segments, antenna 2 with calceoli, and epimeral plates 2 and 3 without long setae on ventral margins.

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New Oriental species of the genus *Stenus* Latreille from the Geneva Museum (Coleoptera: Staphylinidae). 284th Contribution to the knowledge of Steninae. - Description of 11 new species: *Stenus* (*Hemistenus*) *agostii* sp. n. (Sumatra), *S.* (*Hemistenus*) *croceipennis* sp. n. (Sumatra), *S.* (s. str.) *cuccodoroi* sp. n. (Papua New Guinea), *S.* (*Hypostenus*) *exsecratus* sp. n. (Sulawesi), *S.* (*Hypostenus*) *kaibesarensis* sp. n. (Moluccas: Kai Besar), *S.* (*Hypostenus*) *kerincimontis* sp. n. (Sumatra), *S.* (*Hemistenus*) *kurbatovi* sp. n. (Burma), *S.* (*Hypostenus*) *radulipenis* sp. n. (Thailand), *S.* (s. str.) *sannifer* (Java, Lombok), *S.* (*Hemistenus*) *schwendingeri* sp. n. (Thailand) and *S.* (*Hypostenus*) *tanimbarensis* sp. n. (Moluccas: Tanimbar).

Key-words: Coleoptera - Staphylinidae - *Stenus* - taxonomy.

EINLEITUNG

Im umfangreichen Staphylinidenmaterial des Genfer Naturhistorischen Museums fand sich eine Anzahl neuer *Stenus*-Arten aus der Orientalis. Von diesen werden hier 11 beschrieben. Sie gehören zu verschiedenen Verwandtschaftsgruppen, wie jeweils in den Einzelbeschreibungen angegeben. Bemerkenswert ist die Tatsache, dass die beiden neuen von den Molukken beschriebenen Arten zeigen, dass die Gruppe des *Stenus gigas* L. Benick östlich der Weber-Linie (vgl. Joly, 2003) eine reiche Differenzierung erfahren hat. - Sofern nicht anders angegeben, befinden sich Holotypen und Paratypen im Muséum d'histoire naturelle de Genève und Paratypen in meiner Sammlung.

Wie in meinen anderen Arbeiten gelten auch hier die folgenden Abkürzungen: aE = average distance between eyes, mittlerer Augenabstand; HT = Holotypus; lEl = greatest length of elytra, größte Elytrenlänge; lE = length of eyes, Augenlänge; lP = length of pronotum, Pronotumlänge; lS = length of suture, Nahtlänge; PM = proportional measurements, Proportionsmaße (1 Einheit = 0,0252 mm); PT = Paratypus; wEl = greatest width of elytra, größte Elytrenbreite; wH = width of head, Kopfbreite; wP = width of pronotum, Halsschildbreite.

SYSTEMATIK

Stenus (s. str.) sannifer sp. n.

Material: ♂-Holotypus und 2 ♀-Paratypen: [INDONESIEN]: JAVA: Maribaya, 22 km NE Bandung, 27.VII.1984, J. Robert (MHNG, 1 PT coll. Puthz); 1 ♂-Paratypus: [INDONESIEN]: LOMBOK: Senaro, N slope of Rinjani, 1100 m, 2.- 5.II.1984, Bolm (Staatliches Museum für Naturkunde, Stuttgart) ; 4 ♀-Paratypen: Mt. Rinjani, Sebnaro, 400 m, waterfalls, 5.XI.1991, Löbl (MHNG, 1 PT coll. Puthz).

Beschreibung: Länge 2,5-3,1 mm (Vorderkörperlänge: 1,6 mm). Schwarz, mäßig glänzend mit leichtem Messingschimmer, Vorderkörper sehr grob und gedrängtdicht bis rugos punktiert, Abdomen grob und sehr dicht punktiert; Beborstung kurz, wenig auffällig. Fühler bräunlichgelb, Kiefertaster gelb, Beine bräunlichgelb, die Schenkelspitzen angedunkelt. Clypeus schwarz, Oberlippe dunkelbraun, ziemlich dicht beborstet.

PM des HT und des ♂-PT von Lombok (in Klammern): wH: 27,5 (30); aE: 16 (17); wP: 21 (23); IP: 20 (23); wEl: 27,5 (31,5); IEl: 25 (28); IS: 19 (22).

Männchen: Schienen ohne Dornen, Hinterschienen in ihren apikalen zwei Dritteln leicht gebogen und innen abgeflacht. Vordersternite ohne Auszeichnungen. 7. Sternit vor dem Hinterrand feiner und dichter als an den Seiten punktiert und beborstet. 8. Sternit (Fig. 2). 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. A e d o e a g u s (Fig. 1), der breite und vergleichsweise kurze Medianlobus ist vorn nach einer gewellten Kontur in eine kurze, dreieckige Spitze verengt; im Innern werden zwei kräftige, distal gesägte, median verbundene Ausstülpungen und eine dünne Tube deutlich. Die Parameren sind viel länger als der Medianlobus und tragen mehrere Gruppen ziemlich langer Borsten.

Weibchen: 8. Sternit zur Hinterrandmitte leicht vorgezogen, abgerundet. Valvifer apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. Die Spermatheka besteht aus einem langen, dünnen, dreimal gewundenen Schlauch und ist insgesamt fast so lang wie ein Valvifer.

Bemerkungen: Diese neue Art gehört in die Gruppe des *S. javanus* Bernhauer (Puthz, 1980: 29) und ist hier die Schwesterart des *S. javanus*. Äußerlich kann ich sie nicht sicher von jenem trennen, zumal sie auch skulpturell variabel ist: die oben genannten Proportionsmaße des HT und des ♂ von Lombok (beide haben identische Aedoeagen) zeigen schon, welche Unterschiede hier auftreten können. Beim HT handelt es sich um ein schlankeres, deutlich glänzendes und am Vorderkörper kaum rugos punktiertes Exemplar, die Stücke aus Lombok dagegen sind robuster, weniger glänzend und am Vorderkörper erheblich rugoser skulptiert. Zu *S. javanus* (dessen HT ich ebenso wie den des synonymen *S. brachycephalus* Cameron noch einmal untersucht habe) kann ich keine sicheren ektoskelettalen Unterscheidungsmerkmale angeben. Der Aedoeagus beider Arten zeigt aber ihren Unterschied (vgl. Fig. 4). Von *S. sannator* Puthz (Nord-Indien, Nepal), dessen Aedoeagus einen ähnlichen Umriss besitzt, trennt man die neue Art durch weniger tief ausgerandetes 8. Sternit des Männchens (vgl. Fig. 3) und durch den anders gestalteten Ausstülpapparat des Medianlobus (vgl. Abb. 6, Puthz, 1991), von *S. kamhaengi* Rougemont durch fehlende Elytrenmakeln, von *S. spongifera* Cameron, *S. riukiensis* Puthz und *S. sannio* Puthz durch weniger breite Stirn und durch seinen vorn stumpfwinklig (also nicht gerundet-) verengten Medianlobus.

Etymologie: Ich nenne die neue Art *sannifer* = grimassentragend, einmal um ihre Verwandtschaft mit den ähnlich benannten Spezies zu signalisieren, dann aber auch um auszudrücken, dass sie äußerlich merklich variabel ist.

***Stenus (s. str.) cuccodoroi* sp. n.**

Material: ♂-Holotypus und 3 ♂♂-, 2 ♀♀-Paratypen: PAPUA NEUGUINEA: Morobe, Biarud Rd., Mt. Saredomo, 2450 n, 9.VI.1992, G. Cuccodoro # 20A (MHNG, 2 PTT coll. Puthz).

Beschreibung: Länge: 2,7-3,7 mm (Vorderkörperlänge: 1,6-1,8 mm). Preußisch-blau-metallisch, glänzend, Vorderkörper sehr grob und sehr dicht punktiert, Abdomen ziemlich grob und mäßig dicht punktiert; Beborstung kurz, wenig auffällig. Fühler hellbraun, die Keule dunkler, Kiefertaster gelb, das 3. Glied wenig dunkler, Beine kastanienbraun, die Schenkelspitzen etwas dunkler. Clypeus metallisch bis schwarz, Oberlippe schwarzbraun, beide ziemlich dicht beborstet.

PM des HT und eines ♂-PT in Klammern: wH: 27,5 (27,8); aE:16 (16); wP: 21,8 (23), IP: 23 (25); wEl: 30 (35); lEl: 27 (33,5); lS: 22 (28).

Männchen: Beine ohne Auszeichnungen. Metasternum abgeflacht, sehr grob, dicht punktiert, Hinterhüftumrandung glatt. Vordersternite ohne Auszeichnungen. 7. Sternit in der hinteren Mitte sehr fein und sehr dicht punktiert und beborstet, Hinter- rand sehr flach ausgerandet. 8. Sternit mit breitrunder Ausrandung etwa im hinteren Zwölftel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. A e d o e a g u s (Fig. 5), Medianlobus stumpf-dreieckig verengt und im Innern mit dünn tubigem Innensack sowie starken Ausstülpungen. Parameren viel länger als der Medianlobus, an ihren Spitzen nur mit zwei subapikalen Borsten.

Weibchen: 8. Sternit breit abgerundet. Valvifer apikolateral mit spitzem Zahn. 10. Tergit abgerundet.

Bemerkungen: Diese neue Art gehört in die Gruppe des *S. toxopei* Cameron (Puthz, 1971: 448f.) und ist hier die Schwesterart des *S. delicatus* Puthz, dem sie in fast allen Punkten grundsätzlich ähnelt. Sie unterscheidet sich jedoch von ihm durch schmälere Kopf (deutlich schmaler als die Elytren) mit flacherer, weniger tief eingesenkter Stirn mit etwas größerer Punktierung (die Punkte erreichen gut den apikalen Querschnitt des 2. Fühlergliedes), durch größere Pronotumpunktierung (die Pronotumpunktierung ist nur wenig feiner als diejenige der Elytren, bei *S. delicatus* ist der Unterschied viel auffälliger) sowie durch den Innenbau (Hakenumriss) des Medianlobus. Von *S. delicatus* Puthz unterscheidet sich die neue Art durch schmälere Kopf, breitere Elytren, weniger grob punktiertes Abdomen und den Aedoeagus. In ihren Proportionen sind die Stücke der Typenserie merklich variabel: ein ♂-Paratypus fällt durch erheblichere Größe und breitere Elytren auf (vgl. o.).

Etymologie: Ich dediziere diese schöne neue Art ihrem Sammler, Herrn Dr G. Cuccodoro (Genf).

***Stenus (Hypostenus) kerincimontis* sp. n.**

Material: ♂-Holotypus und 1 ♀-Paratypus: [INDONESIEN]: SUMATRA: Jambi, Mt. Kerinci, 3300 m, 12.XI.1989, Agosti, Löbl & Burckhardt # 12a (MHNG, PT coll. Puthz); 1 ♀-Paratypus: ibidem 2100 m, 14.XI.1989, idem # 16 (MHNG).

Beschreibung: Länge: 2,8-3,6 mm (Vorderkörperlänge: 1,7 mm). Brachypter, schwarz, Elytren mit bräunlichem Anflug, schwach glänzend, Stirn ziemlich grob und

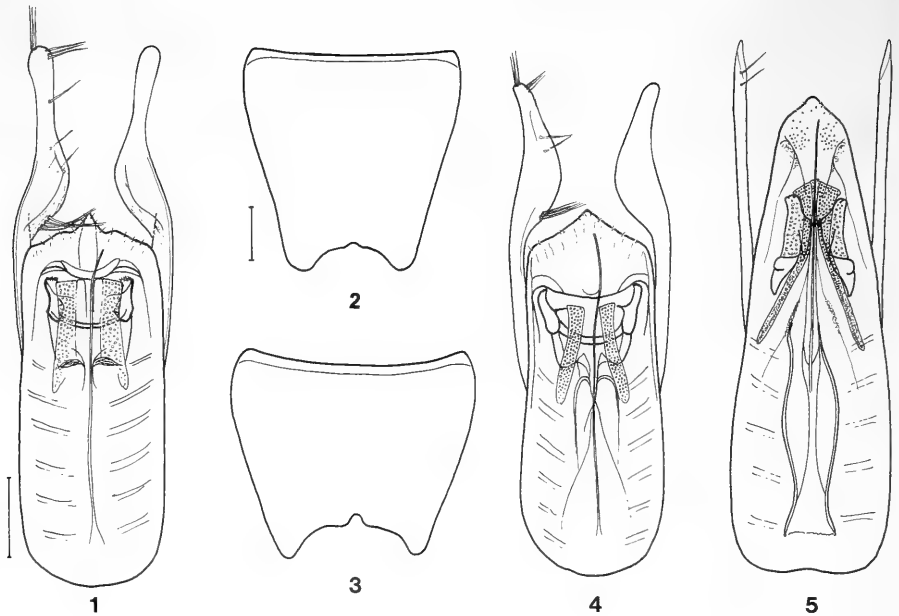


FIG. 1-5

Ventralansicht der Aedoeagen (1, 4, 5) und 8. Sternit der Männchen (2, 3) von *Stenus* (s. str.) *sannifer* sp. n. (PT: 1, 2), *S. sannator* Puthz (3), *S. javanus* Bernhauer (HT von *S. brachycephalus* Cameron, 4) und *S.* (s. str.) *cuccodoroi* sp. n. (PT, 5). - Maßstab = 0,1 mm.

dicht punktiert, Pronotum grob und dicht punktiert, Elytren sehr grob und dicht punktiert, Abdomen ziemlich grob (vorn) bis fein (hinten), überall dicht punktiert. Fühler gelb, die Keule gebräunt, Kiefertaster gelb bis rötlichgelb, Beine bräunlichgelb, Schenkel- und Tarsengliedspitzen kaum dunkler. Clypeus schwarz, Oberlippe schwarzbraun, heller gesäumt, beide spärlich beborstet. Paraglossen oval.

PM des HT: wH: 35; aE: 17; wP: 25; lP: 26; wEl: 31; lEl: 29; lS: 20.

Männchen: Beine ohne Auszeichnungen. Metasternum leicht eingedrückt, grob und dicht auf eng genetztem Grund punktiert, Hinterhüftumrandung innen mit mehreren mäßig feinen Punkten. Vordersternite einfach. 7. Sternit in der hinteren Mitte sehr fein und dicht punktiert und beborstet, Hinterrand kaum erkennbar flach ausgerandet. 8. Sternit mit kleinem rundem Ausschnitt etwa im hinteren Achtzehntel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. *Aedoeagus* (Fig. 8), Medianlobus vorn konvex verengt, im Innern mit stark sklerotisiertem Innensack und median kurz verbundenen Ausstülpungen (Fig. 10). Parameren viel länger als der Medianlobus, in ihrer Spitzenhälfte lang verschmälert, mit zwei Borstengruppen (7, 5).

Weibchen: 8. Sternit zur Hinterrandmitte dreieckig vorgezogen. Valvifer apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. Spermatheka (Fig. 9), etwas kürzer als der stärker sklerotisierte distale Teil des Valvifers.

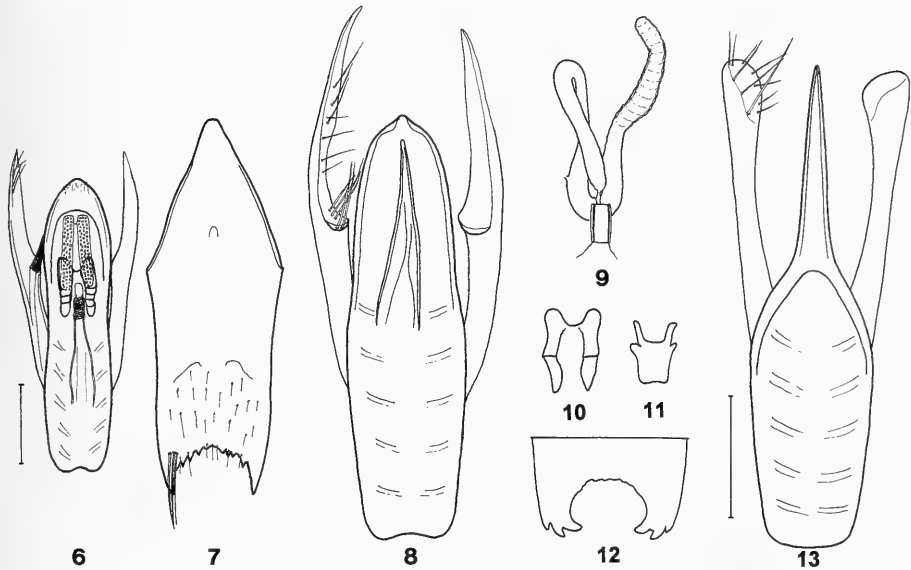


FIG. 6-13

Ventralansicht der Aedoeagen, zum Teil ohne Innenkörper, weil ausgestülpt (6, 8, 13), 9. Sternit des Männchens (7, 12), Spermatheka (9) und Ausstülpphenapparat des Medianlobus (10, 11) von *Stenus* (*Hypostenus*) *exsecratus* sp. n. (HT, 6, 7), *S.* (*Hypostenus*) *kerincimontis* sp. n. (8-10), *S.* (*Hemistenus*) *schwendingeri* sp. n. (HT, 11-13). - Maßstab = 0,1 mm (6= 7-10; 13= 11, 12).

Kopf deutlich breiter als die Elytren, Stirn ziemlich schmal mit deutlichen Längsfurchen, Mittelteil gut so breit wie jedes der Seitenstücke, breitrund erhoben, erreicht fast das Augeninnenrandniveau. Punktierung ziemlich grob und sehr dicht, mittlerer Punktdurchmesser gut so groß wie der mittlere Querschnitt des 3. Fühlergliedes, Punktabstände fast überall kleiner als die Punktradien. Fühler schlank, zurückgelegt knapp den Pronotumhinterrand überragend, vorletzte Glieder etwa eineinhalb mal so lang wie breit. Pronotum kaum länger als breit, seitlich kräftig gewölbt, hinten deutlich konkav verengt. Eine abgekürzte mittlere Längsfurche und seitliche Schrägeindrücke mäßig deutlich. Punktierung gröber als auf der Stirn, dicht, mittlerer Punktdurchmesser gut so groß wie der größte Querschnitt des 3. Fühlergliedes, aber kleiner als der apikale Querschnitt des 2. Fühlergliedes, die glänzenden Punktzwischenräume fast überall (wenig) kleiner als die Punktradien. Elytren rechteckig mit ausgeprägten Schultern, deutlich schmaler als der Kopf und deutlich breiter als lang, die Seiten etwas, gerade, erweitert, Hinterrand tiefrund ausgerandet; keine Eindrücke. Punktierung sehr grob und dicht, aber getrennt, mittlerer Punktdurchmesser so groß wie der mittlere Querschnitt des 2. Fühlergliedes, die genetzten Punktzwischenräume kleiner als die Punktradien. Abdomen stark gewölbt, ellipsoid, die Segmente ohne deutliche seitliche Trennungslinie, wenn auch die unterschiedliche Anordnung der dorsalen und der ventralen Punktierung eine solche vortäuscht. Basale Querrfurchen der ersten

Segmente ziemlich tief, 7. Tergit mit rudimentärem apikalem Hautsaum (ungeflügelte Art). Die Punktierung der ersten Tergite ist jeweils vorn etwa so grob wie auf der Stirn, dicht, nahe dem Hinterrand feiner, das 7. Tergit ist fein und ziemlich dicht punktiert, die Punkte sind etwas kleiner als eine Augeninnenrandfacette, ihre Abstände gut punktgroß. Das 10. Tergit ist fein und mäßig dicht punktiert. Beine schlank, Hintertarsen mehr als zwei Drittel schienenlang, ihr 1. Glied ist deutlich länger als die beiden folgenden zusammengenommen, erheblich länger als das Klauenglied; das 4. Glied ist lang und schmal gelappt. Die Stirn zeigt allenfalls Netzungsspuren, das Pronotum ist ungenetzt, Elytren und Abdomen mehr oder weniger deutlich genetzt.

Bemerkungen: Diese neue Art ist genitaliter den Spezies *S. voraginosus* L. Benick (Java) und *S. exsecratus* sp. n. (Sulawesi) sehr ähnlich, vom ersteren unterscheidet sie sich durch robusteren Bau und die weniger grobe Punktierung des Vorderkörpers, vom zweiten durch kürzere Elytren, gröbere Punktierung von Pronotum und Elytren und weniger dicht punktiertes Abdomen, von beiden durch die Sexualcharaktere. Von allen anderen orientalischen Hypostenen durch die Kombination der Merkmale: einfaches 10. Tergit, apikolateral spitzes 9. Sternum, fehlende Elytrenmakeln, breiten Kopf, helle Beine und ihre geringe Größe. Sie ähnelt habituell den (*Hemistenus*-) Arten *S. aeneopullus* Puthz, *S. iniustus* Puthz und *S. vulcanus* Rouge-mont, die aber alle nur eine flache Stirnmitte (keinen breit erhobenen Mittelteil) besitzen; von *S. despectus* L. Benick unterscheidet sie sich durch nahezu rechteckige, also nicht lang-trapezoide Elytren, von allen diesen durch apikolateral einspitziges 9. Sternum und die fehlende Seitenrandung des Abdomens, schließlich von *S. pilicornis* Fauvel, der ebenfalls auf dem Mt. Kerinci lebt, durch feinere Stirnpunktierung, ungerandetes Abdomen und die Sexualcharaktere.

Etymologie: Der Name bezeichnet die Herkunft der neuen Art.

Stenus (Hypostenus) exsecratus sp. n.

Material: ♂-Holotypus: [INDONESIEN]: SULAWESI: Gunang Mogogonia Pa 1080 m, Utara, X.1985, R. W. Hornabrook (coll. Puthz im MHNG).

Beschreibung: Länge: 2,6-3,4 mm (Vorderkörperlänge: 1,6 mm). Schwarz mit leichtem Brauneinschlag, schwach schimmernd, grob und überall sehr dicht punktiert, Beborstung kurz, nur am Abdomen deutlich. Fühler gelb, die Keule wenig dunkler, Kiefertaster gelb, Beine gelblich, die Schenkel zur Spitze gelblichbraun. Clypeus schwarz, Oberlippe dunkelbraun, heller gesäumt, beide spärlich beborstet.

PM des HT: wH: 29; aE: 15; wP: 22; IP: 22; wEl: 29; lEl: 29; IS: 23.

Männchen: Beine ohne Auszeichnungen. Metasternum grob und dicht auf glänzendem Grund punktiert. Vordersternite einfach. 7. Sternit median abgeflacht und daselbst sehr fein und dicht punktiert und beborstet. 8. Sternit am Hinterrand kaum erkennbar flach ausgerandet. 9. Sternit (Fig. 7). 10. Tergit breit abgerundet. A e d o e a g u s (Fig. 6), Medianlobus vorn abgerundet, im Innern mit stark sklerotisiertem Innensack und großen, median kurz verbundenen Ausstülpungen. Parameren viel länger als der Medianlobus, zur Spitze lang verschmälert und mit zwei getrennten Borstengruppen.

Weibchen: unbekannt.

Kopf etwa so breit wie die Elytren, Stirn schmal mit deutlichen Längsfurchen, Mittelteil so breit wie jedes der Seitenstücke, deutlich, aber wenig, breitrund erhoben, erreicht nicht die Höhe der Augeninnenränder. Punktierung grob und überall sehr dicht, mittlerer Punktdurchmesser gut so groß wie der mittlere Querschnitt des 3. Fühlergliedes, die scharfen Punktzwischenräume viel kleiner als die Punktradien. Fühler schlank, zurückgelegt den Hinterrand des Pronotums erreichend, vorletzte Glieder wenig länger als breit. Pronotum so lang wie breit, vorn seitlich kräftig konvex, hinten deutlich eingeschnürt, mit einer vorn und hinten abgekürzten deutlichen Mittelfurche, seitlich kaum uneben. Punktierung so grob und ebenso dicht wie auf der Stirn, die Punkte sind aber tiefer eingestochen. Elytren so breit wie der Kopf, quadratisch, so lang wie breit, Schultern rechteckig, Schultereindrücke und ein vorderer Nahteindruck deutlich. Punktierung deutlich etwas gröber als am Pronotum, überall sehr dicht, mittlerer Punktdurchmesser so groß wie der apikale Querschnitt des 2. Fühlergliedes. Abdomen breit-zylindrisch, eine Seitenrandung nur skulpturell angedeutet, nicht klar ausgeprägt, basale Quereinschnürungen der ersten Segmente tief, 7. Tergit mit deutlichem apikalem Hautsaum (die Art ist makropter). Punktierung vorn etwa so grob wie auf der Stirn, nach hinten deutlich feiner, überall sehr dicht, auf dem 7. Tergit sind die Punkte wenig feiner als eine Augeninnenrandfacette, ihre Abstände fast so groß wie die Punkte, das 10. Tergit ist sehr fein und spärlich punktiert. Beine schlank, Hintertarsen drei Viertel schienenlang, ihr 1. Glied fast so lang wie die drei folgenden zusammengekommen, erheblich länger als das Klauenglied; 4. Glied schmal und tief gelappt. Stirn mit Netzungsspuren, Pronotum und Elytren zwischen den Punkten glatt, das gesamte Abdomen deutlich genetzt.

Bemerkungen: Diese neue Art ist (genitaliter) die Schwesterart des *S. voraginosus* L. Benick. Sie unterscheidet sich von ihm äußerlich sofort durch ihre größeren Elytren und die erheblich feinere und vor allem am Abdomen viel dichtere Punktierung sowie durch das seitlich ungerandete Abdomen (*S. voraginosus* besitzt eine sehr dünne, aber vollständige Seitenlinie, wenn auch keine Trennung in Tergite und Sternite). Von allen orientalischen (*Hypostenus*-) Arten unterscheidet sie sich ebenso wie *S. kerincimontis* (vgl. o.), von diesem durch größere Elytren, viel dichtere Abdominalpunktierung und die Sexualcharaktere. Habituell ähnelt sie den (*Hemistenus*-) Spezies *S. absurdus* Puthz, *S. guru* Puthz, *S. inconspicuus* Cameron und *S. perfidiosus* Puthz, die auch alle ein apikolateral spitzes 9. Sternit besitzen, die aber entweder eine gröber punktierte oder flache Stirn und/oder gröber punktierte Abdomina aufweisen, ganz abgesehen von den Sexualcharakteren.

Etymologie: Ich nenne diese Art „verwünscht“ (lat. *exsecratus*), weil sie sich äußerlich so stark von ihren Nahverwandten unterscheidet und man ihre Verwandtschaft erst nach Genitaluntersuchung überrascht erkennt.

Stenus (Hypostenus) radulipenis sp. n.

Material: ♂ -Holotypus: THAILAND: Taksin Maharat National Park [westlich Tak], 1000 m, 9.II.1993, Schwendinger.

Beschreibung: Länge: 4,0-5,0 mm (Vorderkörperlänge: 2,4 mm). Schwarz, Elytren mit großer, ovaler, orangegelber Makel, Vorderkörper fast matt, Abdomen etwas glänzend, Stirn grob und sehr dicht punktiert (keine Glättungen), Pronotum sehr

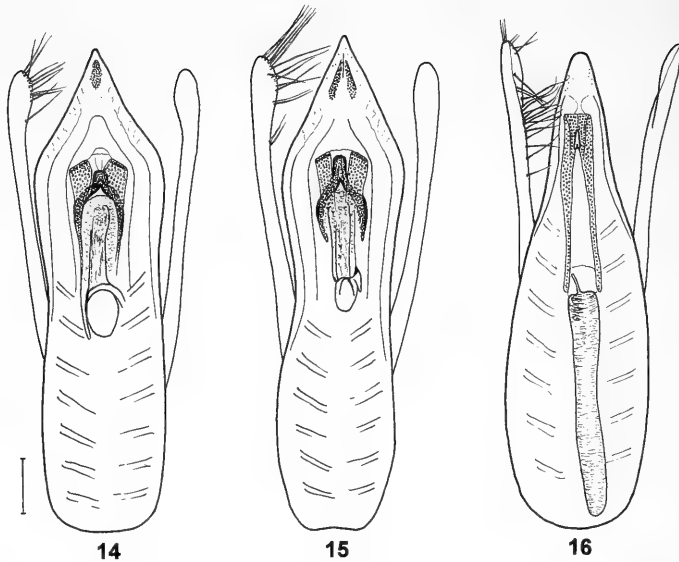


FIG. 14-16

Ventralansicht der Aedoeagen von *Stenus* (*Hypostenus*) *kaibesarensis* sp. n. (HT, 14), *S.* (*Hypostenus*) *tanimbarensis* sp. n. (HT, 15) und *S.* (*Hemistenus*) *kurbatovi* sp. n. (HT, 16). - Maßstab = 0,1 mm.

grob, sehr tief eingestochen und sehr dicht, überall kurz-zusammenfließend skulptiert, außerdem mit mehreren tiefen Eindrücken, Elytren sehr grob und äußerst dicht, leicht zusammenfließend punktiert, Abdomen vorn grob und sehr dicht, hinten wenig fein und dicht auf netzungsfreiem Grund punktiert; Beborstung kurz, wenig auffällig. Fühlerbasis rötlichgelb, die Keule dunkler, Kiefertaster rötlichgelb, Beine rötlichgelb, die Schenkelspitzen etwas dunkler. Clypeus schwarz, Oberlippe dunkelbraun bis (vorn) heller, Clypeus dicht, Oberlippe dünner beborstet.

PM des HT: wH: 47; aE: 23; wP: 33; lP: 34; wEl: 46; lEl: 44; lS: 32.

Männchen: Mittelschienen mit kleinem Apikaldorn, Hinterschienen mit kleinem Präapikaldorn. Vordersternite ohne Auszeichnungen, 7. Sternit median feiner und dichter als an den Seiten punktiert und beborstet, Hinterrand kaum erkennbar flach ausgerandet. 8. Sternit mit geschwungen-spitzwinkligem Ausschnitt fast im hinteren Fünftel. 9. Sternit apikolateral mit kurzem, spitzem Zahn. 10. Tergit sehr breit abgerundet. Aedoeagus (Fig. 17), die Apikalpartie des Medianlobus etwa lanzettlich, leicht dorsad gebogen und dicht mit kurzen Sinnesborsten versehen. Im Innern wird die für die *guttalis*-Gruppe kennzeichnende dreieckige Spange erkennbar. Parameren deutlich länger als der Medianlobus, zur Spitze erweitert und daselbst mit zahlreichen mäßig langen Borsten versehen.

Weibchen: unbekannt.

Bemerkungen: Diese neue Art gehört in die *guttalis*-Gruppe (Puthz, 1988: 635) und ist hier die Schwesterart des *S. subguttalis* Puthz. In ihren ektoskelettalen Merkmalen ähnelt sie mehreren Arten ihrer Gruppe stark, so dass es zu ihrer Charak-

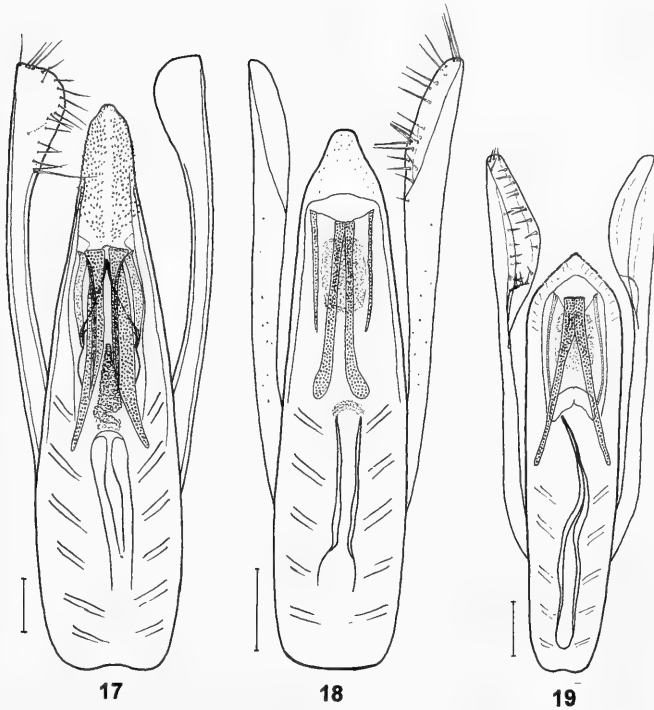


FIG. 17-19

Ventralansichten der Aedoeagen von *Stenus (Hypostenus) radulipenis* sp. n. (HT, 17), *S. (Hemistenus) croceipennis* sp. n. (PT, 18) und *S. (Hemistenus) agostii* sp. n. (PT, 19). - Maßstab = 0,1 mm.

terisierung ausreicht, neben einer Kurzbeschreibung die wesentlichen Unterscheidungsmerkmale zu nennen. Sie unterscheidet sich von ihren (*Hypostenus*-) Verwandten *S. asperrimus* L. Benick, *S. bivulneratus* Motschulsky, *S. burckhardti* Rougemont, *S. guttalis* Fauvel und *S. iniquus* L. Benick durch ungenetztes Abdomen, von *S. asperrimus*, *S. iniquus* und *S. subiniquus* Puthz durch ihre Elytrenmakeln, schließlich von *S. subguttalis* Puthz und *S. variipennis* Rougemont durch breitere und längere, mehr rundlich-rechteckige (also nicht trapezoide) Elytren, länglichere (ovale) Elytrenmakeln und weniger grob und dicht punktierte Abdomenspitze (Punktabstände bei der neuen Art meist etwa so groß wie die Punkte), von allen genannten Spezies durch den Aedoeagus.

Etymologie: Weil die Apikalpartie des Medianlobus an eine Radula erinnert, nenne ich die neue Art *radulipenis*.

***Stenus (Hypostenus) kaibesarensis* sp. n.**

Material: ♂ -Holotypus: [INDONESIEN]: MALUC: Kai Besar G., Tukrau, 300 m, leaf litter, 7.IX.1991, D. Agosti., F911074, # 8 (MHNG); 1 ♂ -Paratypus: Kai Besar: Bombay (E. of Elat), G. Dab, 3.IX.1991, D. Agosti, F911018, # 4 (coll. Puthz).

Beschreibung: Länge: 4,5-5,7 mm (Vorderkörperlänge: 2,3 mm). Brachypter, blaumetallisch, ziemlich glänzend, Stirn grob und ziemlich weitläufig punktiert, Pronotum und Elytren sehr grob und sehr dicht, aber getrennt punktiert, Abdomen grob und ziemlich dicht punktiert; Beborstung kurz, wenig auffällig. Fühler hellbraun, die Keule wenig dunkler, Kiefertaster rötlichgelb, Beine rötlichgelb, die Knie und die Tarsen wenig dunkler. Clypeus blaumetallisch bis schwarzbraun, Oberlippe dunkelbraun, heller gesäumt, beide mäßig dicht beborstet.

PM des HT: wH: 45,5; aE: 26; wP: 31,5; IP: 35; wEl: 41; IEl: 34,5; IS: 22.

Männchen: Beine ohne Auszeichnungen. Metasternum abgeflacht, grob und ziemlich dicht punktiert. Vordersternite grob und dicht punktiert. 7. Sternit in der hinteren Mitte feiner (aber immer noch ziemlich grob) und dichter als an den Seiten punktiert. 8. Sternit mit geschwungen-stumpfwinkligem Ausschnitt etwa im hinteren Elftel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit abgerundet. *A e d o e a g u s* (Fig. 14) mit spitzwinklig verengtem Medianlobus, dieser vorn mit einem ventralen Feld dicht stehender Sinnesborsten. Parameren kürzer als der Medianlobus, apikal etwas verbreitert und daselbst mit ca. 10 kräftigen Borsten.

Weibchen: unbekannt.

Kopf deutlich breiter als die Elytren, Stirn mäßig breit mit flachen Längsfurchen und einem kaum erhobenen Mittelteil, der etwas schmaler als jedes der Seitenstücke ist. Punktierung grob, mittlerer Punktdurchmesser gut so groß wie der basale Querschnitt des 3. Fühlergliedes, auf den Seiten meist dicht (Punktabstände hier größer als die Punktradien), neben dem hinteren Augeninnenrand mit kleiner punktfreier Partie, Stirnmitte nur mit wenigen, zerstreuten Punkten, überwiegend punktfrei. Fühler kurz, zurückgelegt bis ins hintere Pronotumdrittel reichend, vorletzte Glieder eineinhalb mal so lang wie breit. Pronotum breit tonnenförmig, deutlich etwas länger als breit, seitlich wenig gewölbt, hinten nur flach konkav verengt, ohne Eindrücke. Punktierung sehr grob und sehr dicht, der mittlere Punktdurchmesser ist nur wenig kleiner als der größte Querschnitt des 2. Fühlergliedes, die Punktwischnräume sind bis auf wenige Ausnahmen überall viel schmaler als die Punktradien. Elytren trapezoid, viel schmaler als der Kopf, erheblich breiter als lang, Schultern schräg, Seiten kräftig nach hinten erweitert, Hinterrand tiefrund ausgerandet; ein flacher Schultereindruck erkennbar. Punktierung ähnlich grob und dicht wie am Pronotum. Abdomen stark gewölbt, fast zylindrisch, die Segmente 4-6 zeigen nur eine ange-deutete seitliche Trennungslinie, die basalen Quereinschnürungen der ersten Segmente sind sehr tief, das 7. Tergit trägt einen reduzierten apikalen Hautsaum. Die Punktierung ist grob und ziemlich dicht, vorn nur wenig gröber als hinten, auf dem 3. Tergit sind die Punkte so groß wie der basale Querschnitt des 3. Fühlergliedes, ihre Abstände etwa punktgroß, auf dem 7. Tergit sind die etwas längs-angezogenen Punkte kaum kleiner, ihre Abstände gut punktgroß, das 10. Tergit ist wenig fein und wenig dicht punktiert. Beine schlank, die Hintertarsen nicht ganz drei Fünftel schienenlang, ihr 1. Glied ist etwas kürzer als die drei folgenden zusammengekommen, deutlich länger als das Klauenglied; das 4. Glied ist tief gelappt. Die Stirn und der überwiegende Teil des Abdomens sind deutlich genetzt, Pronotum und Elytren sowie das 8. Tergit zeigen nur Netzungsspuren, 10. Tergit ungenetzt.

Bemerkungen: Diese neue Art gehört in die Gruppe des *S. gigas* L. Benick (Puthz, 1971: 449) und hier in die Nähe des *S. magnificus* L. Benick. Sie unterscheidet

sich von all ihren Nahverwandten durch ihre kurzen, breiten Elytren, ihre sehr grobe Vorderkörperpunktierung, ihre Netzung und durch den Aedoeagus.

Etymologie: Der Name dieser Art bezeichnet ihre Herkunft von der Molukkeninsel Kai Besar.

Stenus (Hypostenus) tanimbarensis sp. n.

Material: ♂-Holotypus und ♀-Paratypus: [INDONESIEN]: MALUC: Tanimbar Island: Yamdena Domaki, NW of Saumlaki, 18.IX.1991, D. Agosti, F911146.

Beschreibung: Länge: 5,0-6,2 mm (Vorderkörperlänge: 2,5 mm). Brachypter, blaugrün bis grasgrünmetallisch, stark glänzend, Stirn mäßig fein und ziemlich weitläufig punktiert, Pronotum und Elytren grob und dicht punktiert, Abdomen mäßig grob und ziemlich weitläufig punktiert; Beborstung kurz, wenig auffällig. Fühler hellbraun, die Keule etwas dunkler, Kiefertaster rötlichgelb, Beine bräunlichgelb, Schenkelspitzen und Tarsen wenig dunkler. Clypeus metallisch bis schwarz, Oberlippe dunkelbraun bis heller, beide mäßig dicht beborstet.

PM des HT: wH: 48; aE: 24; wP: 33; IP: 35; wEl: 42; IEl: 38; IS: 24.

Männchen: Beine ohne Auszeichnungen. Metasternum abgeflacht, grob und mäßig dicht punktiert. 6. Sternit median feiner und dichter als an den Seiten punktiert und beborstet. 7. Sternit median sehr fein und sehr dicht punktiert und beborstet. 8. Sternit mit stumpfwinkligem Ausschnitt etwa im hinteren Achtel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit zum Hinterrand rundlich vorgezogen. *Aedoeagus* (Fig. 15) ähnlich dem des *S. kaibesarensis*, Medianlobus aber etwas schlanker, apikoventral mit zwei Sinnesborstenfeldern, Parameren stärker und länger beborstet.

Weibchen: 8. Sternit schmal abgerundet. Valvifer apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet.

Kopf ähnlich wie bei *S. kaibesarensis*, Stirn jedoch schmaler, Mittelteil ebenfalls nur sehr flach gewölbt, Punktierung aber viel feiner: die größten Punkte sind deutlich kleiner als der basale Querschnitt des 3. Fühlergliedes, etwa so groß wie eine Augenfacette, die kleinsten (auf der hinteren Partie der Seitenstücke) erheblich kleiner; die Stirnmitte ist überwiegend punktfrei, auf den Seitenstücken stehen die Punkte im mittleren Bereich dicht, ihre Abstände werden aber nach vorn und vor allem nach hinten erheblich größer. Fühler und Pronotumumriss ähnlich wie bei der verglichenen Art, die Punktierung des Pronotums zwar grob, aber viel feiner als bei *S. kaibesarensis*, der mittlere Punktdurchmesser liegt etwas über dem basalen Querschnitt des 3. Fühlergliedes, die glänzenden Punktzwischenräume sind oft kaum schmaler als die Punktradien, ausnahmsweise auch einmal punktgroß. Die Elytren sind ebenfalls trapezoid und im Umriss ähnlich wie bei *S. kaibesarensis*, ihre Punktierung aber weniger grob und nicht so gedrängt, die Punkte leicht quer-angezogen, der mittlere Punktdurchmesser entspricht etwa dem größten Querschnitt des 3. Fühlergliedes, die Punktabstände sind auf der Scheibe deutlich etwas schmaler als die Punktradien, seitlich so groß oder auch größer; in der Elytrenhinterhälfte stehen die Punkte in leichten Querreihen angeordnet. Abdomen prinzipiell wie bei *S. kaibesarensis*, auch die Punktierung. Auch die Beine etwa wie bei der verglichenen Art. Stirn mit

Netzungsspuren, Pronotum und Elytren zwischen den Punkten glatt, Abdomen mit kaum erkennbar flacher Netzung.

Bemerkungen: Diese neue Art unterscheidet sich von ihren Nahverwandten durch ihre kurzen, trapezoiden Elytren, ihr vergleichsweise kurzes Pronotum und die Sexualcharaktere. Sie ähnelt am meisten den neuguineensischen Spezies *S. cyaneotogatus* Puthz und *S. magnificus* L. Benick.

Etymologie: Der Namen der neuen Art bezeichnet ihre Herkunft von der Molukkeninsel Tanimbar.

***Stenus (Hemistenus) schwendingeri* sp. n.**

Material: ♂-Holotypus und 2 ♀-Paratypen: THAILAND: Huay Nam Dang, Mae Taeng District, 1400 m, 17.XII.1990, P. Schwendinger (MHNG, 1 PT coll. Puthz).

Beschreibung: Länge: 2,6-3,4 mm (Vorderkörperlänge: 1,6-1,7 mm). Schwarz mit leichtem Bronzeschimmer, schwach schimmernd, Vorderkörper grob und sehr dicht punktiert, Abdomen vorn ziemlich grob, hinten mäßig fein, überall sehr dicht punktiert; Beborstung kurz, wenig auffällig. Fühler schmutziggelb, die Keule gebräunt, Kiefertaster rötlichgelb, Beine einfarbig bräunlichgelb. Clypeus schwarz, Oberlippe braunschwarz, beide dünn beborstet. Paraglossen oval.

PM des HT: wH: 28,5; aE: 14; wP: 21; iP: 21,5; wEl: 28,3; iEl: 30; IS: 25.

Männchen: Beine ohne Auszeichnungen. Metasternum flach gewölbt, grob und dicht auf glänzendem Grund punktiert. Vordersternite einfach. 7. Sternit in der hinteren Mitte sehr fein und dicht, flach punktiert und beborstet. 8. Sternit mit kleinem Apikalausschnitt etwa im hinteren Achtzehntel. 9. Sternit apikolateral dreizähngesägt (Fig. 12). 10. Tergit abgerundet. *A e d o e a g u s* (Fig. 13), Medianlobus in seiner Vorderhälfte nadeldünn, im Innern mit einem tubigen Innensack und einer deutlich sklerotisierten Ausstülpung (Fig. 11). Parameren etwa so lang wie der Medianlobus, an ihren Spitzen etwas löffelförmig erweitert und daselbst mit 3+7 Borsten, von denen eine besonders lang und kräftig ist.

Weibchen: 8. Sternit am Hinterrand breit abgerundet. Valvifer apikolateral dreizähngig. 10. Tergit abgerundet. Spermatheka aus einem dünnen, vielfach gewundenen Schlauch ("Schlauchgewirr") mit einem kräftig sklerotisierten, ziemlich langen Einfüllstutzen bestehend, insgesamt fast so lang wie ein Valvifer.

Kopf beim Männchen gut so breit wie die Elytren, beim Weibchen etwas schmaler, Stirn schmal, eingesenkt und innen ganz flach, Punktierung grob und sehr dicht, mittlerer Punktdurchmesser fast so groß wie der apikale Querschnitt des 2. Fühlergliedes, Punktzwischenräume viel kleiner als die Punktradien. Fühler schlank, zurückgelegt den Pronotumhinterrand überragend, vorletzte Glieder nicht ganz doppelt so lang wie breit. Pronotum gut so lang wie breit, in der Vorderhälfte seitlich deutlich konvex, hinten deutlich, aber nicht stark, konkav eingeschnürt; keine Eindrücke. Punktierung sehr regelmäßig, tief eingestochen, so grob wie auf der Stirn, äußerst dicht. Elytren etwa quadratisch, etwas länger als breit, Naht- und Schultereindruck flach. Punktierung auffallend regelmäßig, grob und sehr dicht, kaum gröber als am Pronotum. Abdomen ellipsoid, Seiten deutlich gerundet, Paratergite des 4. Segments nicht ganz so breit wie das 2. Fühlerglied, leicht ventrad geneigt und nur mit einzelnen

Punkten. Basale Querfurchen der ersten Tergite ziemlich tief, 7. Tergit mit deutlichem apikalem Hautsaum (die Art ist voll geflügelt). Punktierung vorn fast so grob wie auf der Stirn, hinten erheblich feiner, auf den einzelnen Tergiten jeweils vorn gröber als hinten; die mittlere Punktgröße der Punkte des 7. Tergits ist so groß wie eine Augeninnenrandfacette; die Punktierung ist überall sehr dicht. 10. Tergit spärlich und zerstreut punktiert. Beine schlank, Hintertarsen fast drei Viertel schienenlang, ihr 1. Glied gut so lang wie die beiden folgenden zusammengenommen, erheblich länger als das Klauenglied; das 4. Glied ist sehr dünn, wenig auffällig gelappt. Stirn und Pronotum zeigen nur Netzungsspuren, Elytren deutlich genetzt, Abdomen vorn flach, hinten deutlicher genetzt.

Bemerkungen: Diese neue Art ist vermutlich die Schwesterart des *S. pallidipes* Cameron, sie sieht ihm zum Verwechseln ähnlich, auch der Medianlobus (nicht jedoch die Parameren) sind sich ähnlich; sie unterscheidet sich von ihm äußerlich nur schwer durch ihre dichtere und etwas weniger grobe Punktierung der Stirnmitte und beim Männchen zusätzlich durch viel flacher ausgerandetes 8. Sternit (*S. pallidipes* zeigt hier einen tiefen spitzwinkligen Ausschnitt gut im hinteren Drittel). Unter den makropteren, ungemakelten orientalischen (*Hemistenus*-) Arten mit apikolateral gesägtem 9. Sternum und eingesenkter Stirnmitte, die eine ähnliche Größe haben, ähnelt die neue Art noch *S. iustus* Puthz, dessen Stirnmitte aber gröber punktiert und dessen vorderes Abdomen ungenetzt ist, sowie *S. humicola* Puthz, der jedoch kleinere Elytren besitzt. Sie ähnelt auch *S. absurdus* Puthz und *S. peratus* Cameron, die aber beide eine erhobene Stirnmitte zeigen, ganz abgesehen von den Sexualcharakteren.

Etymologie: Mit ihrem Namen ehre ich ihren verdienstvollen Sammler, Herrn P. Schwendinger (Genf).

Stenus (Hemistenus) kurbatovi sp. n.

Material: ♂-Holotypus und 4 ♂♂-Paratypen: BURMA: E Mandalay, env. Maymyo, 700 m, 5.III.1996, Kurbatov (MHNG, 1 PT coll. Puthz).

Beschreibung: Länge: 4,5-6,0 mm (Vorderkörperlänge: 2,5 mm). Schwarz, matt, jede Elytre mit einem ziemlich großen, ovalen, orangeroten Fleck, Stirn grob und sehr dicht punktiert, Pronotum sehr grob und sehr dicht, zum Teil zusammenfließend skulptiert, Elytren sehr grob, äußerst dicht, rau, kurz-zusammenfließend skulptiert, Abdomen vorn grob und dicht, hinten wenig fein und ziemlich dicht punktiert; Beborstung kurz, wenig auffällig. Fühler mittelbraun, die Keule wenig dunkler, Kiefertaster rötlichgelb, Beine hellbraun, Schenkel an den Knien wenig dunkler. Clypeus schwarz, Oberlippe dunkelbraun, Clypeus ziemlich dicht, Oberlippe dünn und spärlich beborstet. Paraglossen oval.

PM des HT: wH:48; aE: 25; wP: 31; IP: 32,5; wEl: 47; IEl: 42; IS: 31.

Männchen: Beine ohne Auszeichnungen. Metasternum gewölbt, wenig fein und ziemlich dicht auf flach genetztem Grund punktiert, Hinterhüftumrandung innen glatt. Vordersternite einfach. 7. Sternit in der hinteren Mitte feiner und dichter als an den Seiten punktiert und beborstet. 8. Sternit mit stumpfwinkligem Ausschnitt etwa im hinteren Fünftel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. A e d o e a g u s (Fig. 16), Medianlobus vorn in eine breit abgerundete Spitze verschmälert, im Innern mit einem breittubigen, distal mit schmalem Rohr versehenen

Innensack und mit einem kleinen, stark sklerotisierten distalen Ausstülpungen. Parameren wenig länger als der Medianlobus, mit etwa 17+7 langen Borsten.

Weibchen: unbekannt.

Bemerkungen: Diese neue Art ist die Schwesterart des *S. dentellus* L. Benick, mit dem sie auch zusammen erbeutet wurde. Sie ähnelt ihm äußerlich zum Verwechseln, besitzt jedoch einen breiteren Kopf und einen größeren Aedoeagus mit anderem Innenbau sowie viel stärker beborstete Parameren. Eine sichere Unterscheidung der beiden Arten dürfte nur mit Hilfe der Genitaluntersuchung möglich sein.

Etymologie: Ich dediziere diese neue Art ihrem verdienstvollen Sammler, Herrn S. A. Kurbatov (Moskau).

***Stenus (Hemistenus) croceipennis* sp. n.**

Material: ♂-Holotypus und 5 ♂♂-, 9 ♀♀-Paratypen: [INDONESIEN]: SUMATRA: Jambi, Mt. Kerinci, 1750- 1850 m, 11.- 12.XI.1989, Agosti, Löbl, Burckhardt # 11 (MHNG, 5 Paratypen coll. Puthz).

Beschreibung: Länge: 4,4-5,6 mm (Vorderkörperlänge: 2,3-2,5 mm). Brachypter, schwarz mit bräunlichem Einschlag und schwachem Messingschimmer, Elytren mit sehr großem, ovalem, gelblichem Fleck, Stirn grob und sehr dicht punktiert, Pronotum sehr grob, tief und sehr eng, leicht zusammenfließend punktiert, Elytren sehr grob und sehr dicht, etwas längs-zusammenfließend punktiert, Abdomen mäßig fein bis sehr fein, fast überall dicht punktiert; Beborstung kurz, kaum auffällig. Fühler rötlichgelb, die Keule verdunkelt, Kiefertaster gelb bis rötlichgelb, Beine rötlichgelb, die Schenkelspitzen und die Tarsengliedspitzen etwas angedunkelt. Clypeus schwarz, Oberlippe schwarzbraun, heller gesäumt, wenig dicht beborstet. Paraglossen koniform.

PM des HT: wH:41; aE: 24; wP: 32; IP: 35,5; wEl: 39; lEl: 37; IS: 26.

Männchen: Beine ohne Auszeichnungen. Metasternum dreieckig eingedrückt, mäßig grob, dicht auf genetztem Grund punktiert und beborstet, Hinterhüftumrandung innen mit wenigen, sehr feinen Punkten. Vordersternite ohne Auszeichnungen. 7. Sternit in der hinteren Mitte abgeflacht, sehr fein und dichter als an den Seiten punktiert und beborstet, Hinterrand kaum erkennbar flach ausgerandet. 8. Sternit mit rundlichem Ausschnitt etwa im hinteren Elftel. 9. Sternit apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. *Aedoeagus* (Fig. 18), Medianlobus vorn mäßig breit abgerundet und im Innern außer einem stark sklerotisierten, breittubigen Innensack ohne weitere, stärker sklerotisierte Elemente. Parameren erheblich länger als der Medianlobus, apikal lang-löffelförmig und faltig und daselbst mit etwa 19 mäßig langen Borsten versehen.

Weibchen: 8. Sternit zur Hinterrandmitte deutlich vorgezogen und daselbst abgerundet. Valvifer apikolateral mit spitzem Zahn. 10. Tergit breit abgerundet. Die Spermatheka besteht aus einem langen, vierfach gewundenen Schlauch und ist insgesamt etwa so lang wie der Valvifer.

Kopf gut so breit wie die Elytren, Stirn sehr breit mit breiten, flachen Längsfurchen, der undeutlich abgesetzte Mittelteil ist so breit wie jedes der Seitenstücke, breitrund erhoben und erreicht gut das Augeninnenrandniveau. Die Punktierung ist grob und sehr dicht, der mittlere Punktdurchmesser erreicht den

größten Querschnitt des 3. Fühlergliedes, die scharfen Punktzwischenräume sind viel kleiner als die Punktradien, nur auf dem hinteren Mittelteil können sie bis punktgroß werden. Fühler schlank, zurückgelegt den Pronotumhinterrand erreichend, vorletzte Glieder gut doppelt so lang wie breit. Pronotum wenig länger als breit, in den vorderen drei Fünfteln seitlich stark konvex, hinten deutlich konkav eingezogen; die Oberseite zeigt mehrere Unebenheiten: eine vorn und hinten abgekürzte mittlere Längsfurche, einen kräftigen seitlichen Quereindruck knapp hinter der Mitte und einen flachen Quereindruck hinter dem Vorderrand. Die Skulptur ist sehr grob und sehr dicht, unterschiedlich kurz-zusammenfließend, der mittlere Punktdurchmesser liegt über dem größten Querschnitt des 3. Fühlergliedes, erreicht aber nicht immer (vor allem direkt in der Mitte nicht) den apikalen Querschnitt des 2. Fühlergliedes, die flach genetzten Punktzwischenräume sind fast überall kleiner als die Punktradien. Die trapezoiden Elytren sind wenig schmaler als der Kopf, deutlich breiter als lang, ihre Seiten hinter den wenig ausgeprägten Schultern kräftig erweitert, ihr Hinterrand ist tief und ausgerandet. Ihre Oberfläche ist etwas uneben, und zwar erscheinen bei den meisten Stücken die großen, gelben Flecken etwas aufgetrieben. Die Flecken können vorn fast bis zur Schulter reichen, hinten berühren sie den Hinterrand, seitlich enden sie am Deckenabfall und von der Naht sind sie in der Elytrenhinterhälfte etwa um die Länge des 2. Hintertarsengliedes getrennt. Die Punktierung ist sehr grob, fließt leicht längs zusammen, überall sehr dicht, ähnlich dicht wie am Pronotum. Abdomen breit elliptisch, Paratergite breit und leicht aufgebogen, diejenigen des 4. Segments so breit wie die Hinterschienen in ihrem basalen Drittel; sie sind mäßig fein, dicht, auch nebeneinander punktiert. Die basalen Querfurchen der ersten Tergite sind tief, das 7. Tergit trägt einen schmalen apikalen Hautsaum (trotz Brachypterie). Die Tergitpunktierung ist vorn mäßig fein und dicht, hinten sehr fein und ziemlich dicht, auf dem 7. Tergit sind die Punkte kleiner als eine innere Augenfacette, ihre Abstände fast doppelt so groß wie die Punkte, das 10. Tergit ist sehr fein und zerstreut punktiert. Beine schlank, Hintertarsen etwa zwei Drittel schienenlang, ihr 1. Glied etwas länger als die beiden folgenden zusammengenommen, deutlich länger als das Klauenglied; das 4. Glied ist lang und schmal gelappt. Die Oberseite des Vorderkörpers ist sehr flach, die des Abdomens dicht und deutlich genetzt.

Bemerkungen: Die neue Art unterscheidet sich von denjenigen (*Hemistenus*-) Arten mit koniformen Paragalossen (vgl. Puthz, 1998: 397 f.), apikolateral spitzem 9. Sternum und kurzen, gemakelten Elytren so: von *S. rafflesi* Rougemont durch gröbere Punktierung des Vorderkörpers und viel weniger gedrängte Abdominalpunktierung, von *S. abdominalis maculosus* L. Benick, *S. cham* Puthz (der ein ähnlich punktiertes Abdomen besitzt), kurzflügligen *S. coronatus* L. Benick, *S. leileri* Puthz und *S. malabarensis* Cameron durch größere Elytrenmakeln, von allen durch die Sexualcharaktere.

Etymologie: Wegen ihrer großen gelben Elytrenmakeln nenne ich diese Art *croceipennis*.

Stenus (Hemistenus) agostii sp. n.

Material: ♂-Holotypus und 5 ♂♂-Paratypen: [INDONESIEN]: SUMATRA: Jambi, Mt. Kerinci, 3000 m, 12.XI.1989, Agosti, Löbl & Burckhardt # 13a; 3 ♂♂-, 2 ♀♀-Paratypen: ibidem, 2500 m, 12.XI.1989, idem # 14; 2 ♂♂-, 3 ♀♀-Paratypen: ibidem 1800-2100 m, 6.-7.III.1991, Bocák & Bocákóva (Naturhistorisches Museum Basel und coll. Puthz).

Beschreibung: Länge: 4,0-5,4 mm (Vorderkörperlänge: 2,3-2,5 mm). Brachypter, schwarz mit schwachem Messingschimmer, Stirn grob und sehr dicht punktiert, Pronotum grob, unregelmäßig, zum Teil zusammenfließend punktiert, Elytren sehr grob und zusammenfließend skulptiert, Abdomen vorn mäßig grob und sehr dicht, hinten fein und dicht punktiert; Beborstung anliegend, wenig auffällig. Fühler rötlichgelb, die Keule gebräunt, Kiefertaster gelb, das 3. Glied verdunkelt, Beine hell rötlichbraun, die Schenkelspitzen (kaum) und die Tarsen dunkler. Clypeus schwarz, Oberlippe braunschwarz, beide wenig dicht beborstet. Paraglossen koniform.

PM des HT: wH: 40,5; aE: 23; wP: 30,5; lP: 32; wEl: 38,5; lEl: 39; lS: 31.

Männchen: Beine ohne Auszeichnungen. Metasternum breit eingedrückt und daselbst mäßig grob, dicht auf genetischem Grund punktiert und beborstet, Hinterhüftumrandung innen fast glatt. 3-6. Sternit median unpunktiert, dicht und flach genetzt. 7. Sternit median leicht abgeflacht, feiner und viel dichter als an den Seiten punktiert und beborstet. 8. Sternit mit schmalem, rundem Ausschnitt etwa im hinteren Achtel. 9. Sternit apikal gesägt. 10. Tergit breit abgerundet. *Aedoeagus* (Fig. 19), der schmale Medianlobus zur Spitze breit-dreieckig verengt; neben einem stark sklerotisierten Innensack wird noch eine wenig stark sklerotisierte Ausstülpung erkennbar. Parameren viel länger als der Medianlobus, an ihren Spitzen lang-löffelförmig und daselbst mit zahlreichen kurzen und kräftigen Borsten versehen.

Weibchen: 8. Sternit am Hinterrand abgerundet, zur Hinterrandmitte kaum vorgezogen. Valvifer apikal gesägt. 10. Tergit breit abgerundet. Die Spermatheka besteht aus einem doppelt S-förmig gewundenen kräftigen Schlauch mit kleinem Blasenanhang und ist etwa zwei Drittel so lang wie der Valvifer.

Kopf deutlich etwas breiter als die Elytren, Stirn ziemlich breit mit flachen Längsfurchen und einem nur schwach erhobenen Mittelteil, der nicht die Höhe der Augeninnenränder erreicht. Punktierung grob und sehr dicht, mittlerer Punktdurchmesser so groß wie der mittlere Querschnitt des 3. Fühlergliedes, die scharfen Punktwahrscheinlichkeiten deutlich kleiner als die Punktradien, in der hinteren Stirnmitte manchmal bis punktgroß. Fühler schlank, zurückgelegt knapp den Pronotumhinterrand überragend, vorletzte Glieder etwas länger als breit. Pronotum wenig länger als breit, knapp hinter der Mitte am breitesten, von dort nach vorn konvex, nach hinten deutlich konkav verengt; außer einer flachen, vorn und hinten abgekürzten (und in der Mitte manchmal etwas verbreiterten) mittleren Längsfurche sind noch mäßig flache Schrägeindrücke knapp hinter der Mitte zu sehen. Die Skulptur ist unregelmäßig, oft kurz zusammenfließend, die Punkte sind unterschiedlich tief eingestochen, ihre Zwischenräume unterschiedlich stark erhoben, die größten Punkte sind etwas gröber als die Stirnpunkte, in der Scheibenmitte stehen meist etwas feinere Punkte. Elytren schmaler als der Kopf, etwas länger als breit, Schultern mäßig eckig, Seiten lang erweitert (Gesamteindruck: lang-trapezoid), Schultereindruck deutlich, hintere Elytrenmitte leicht aufgetrieben. Die Skulptur ist, besonders auf der Hinterhälfte, noch unregelmäßiger und hier auch länger-zusammenfließend als am Pronotum und meist auch etwas gröber als dort. Das breit-elliptische Abdomen besitzt breite, dorsad aufgeboogene Paratergite, diejenigen des 4. Segments sind gut so breit wie die Hinterschienen an ihrer Basis, sie sind dicht, wenig fein, auch nebeneinander punktiert. Die basalen Querrinnen der ersten Tergite sind tief, das 7. Tergit trägt einen breiten apikalen

Hautsaum (obwohl die Art brachypter ist). Die Punktierung ist überall sehr dicht (vorn) bis dicht (hinten), die Punkte des 3. Tergits sind so groß wie der basale Querschnitt des 3. Fühlergliedes, diejenigen des 7. Tergits etwas feiner als eine Augeninnenrandfacette, ihre Abstände hier gut punktgroß. Das 10. Tergit ist ziemlich fein und weitläufig punktiert. An den kräftigen Beinen sind die Hintertarsen nicht ganz zwei Drittel schienenlang, ihr 1. Glied ist deutlich länger als die beiden folgenden zusammengenommen, viel länger als das Klauenglied; das 4. Glied ist lang und schmal gelappt. Die Oberseite des Vorderkörpers zeigt nur flache Netzungsspuren, das ganze Abdomen ist flach, aber deutlich genetzt.

Bemerkungen: Die neue Art ist die Schwesterart des philippinischen *S. contrusus* L. Benick; von ihm unterscheidet sie sich durch breiteren Kopf, flachere Stirnmitte, feiner und dichter punktiertes Abdomen und das gesägte 9. Sternum. Die Aedoeagen beider Arten sind sich sehr ähnlich.

Etymologie: Ich dediziere diese neue Art einem ihrer Sammler, Herrn D. Agosti (Zürich).

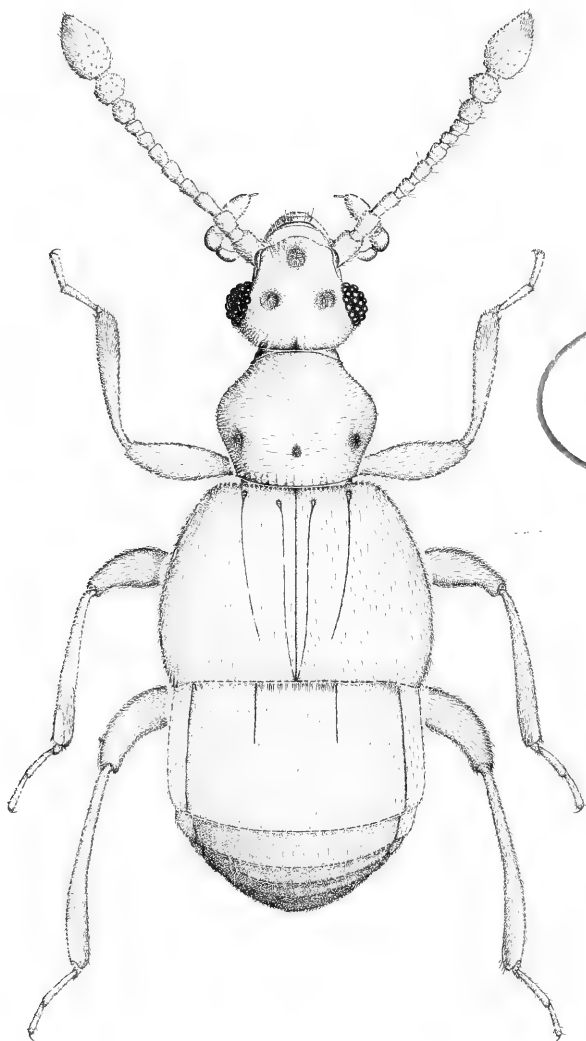
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REVISION DER PALÄARKTISCHEN ARTEN
DER GATTUNG *BRACHYGLUTA* THOMSON, 1859,
1. TEIL
(COLEOPTERA STAPHYLINIDAE)



Giorgio Sabella, Christoph Bückle, Volker Brachat & Claude Besuchet

Giorgio SABELLA, Christoph BÜCKLE, Volker BRACHAT & Claude BESUCHET

REVISION DER PALÄARKTISCHEN ARTEN DER
GATTUNG *BRACHYGLUTA* THOMSON, 1859,
1. Teil: Arten mit sekundären männlichen
Geschlechtsmerkmalen auf den Abdominaltergiten
(Coleoptera, Staphylinidae, Pselaphinae).

The systematic position of the genus *Brachygluta* within the Pselaphinae and Brachyglutini is specified. The distribution of the genus covers mainly the Holarctic region, with two species known from the Afrotropical region. Detailed descriptions and 669 illustrations of the morphology of the external and internal skeleton structures as well as of the aedeagus are given for each species. Some particular of integument structure and pilosity are reproduced by scanning electron microscope photographs. Available information on biology, ecology and ontogenesis is summarized. The external morphology and the characteristics of the aedeagus are precisely described for the 75 Palaearctic (sub)species exhibiting secondary male sexual characters on abdominal tergites. Distribution maps are given for all species.

Twenty-one species are described as new for science, four synonymies are established, six subspecies are elevated at species level, and, finally, two new combinations are proposed. A list of species and their synonyms is provided. The descriptions are in German, the identification keys are in French and English.

This publication is addressed to systematicians, ecologists, entomologists interested in faunistic research as well as to libraries of museums of natural history and entomological institutes.

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***Nesticella marapu* sp. n., a blind nesticid (Araneae: Nesticidae) from Sumba, Indonesia**

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***Nesticella marapu* sp. n., a blind nesticid (Araneae: Nesticidae) from Sumba, Indonesia.** - A new species of the genus *Nesticella* is described from both sexes. It is characterised by the presence of a beak-shaped paracymbium. It has long legs and weak pigmentation but lacks eyes.

Key-words: *Nesticella* - Nesticidae - new species - troglobit - caves.

INTRODUCTION

The spider family Nesticidae has been revised by Lehtinen & Saaristo (1980). It is the sister taxon of Theridiidae (Coddington, 1986; Coddington, 1989; Coddington, 1990; Griswold *et al.*, 1998). Spiders of both families construct webs with a supporting structure and with lines under tension termed gumfooted lines. The bases of these gumfooted lines are the only parts of the web that contain viscid silk (Benjamin & Zschokke, 2002; Benjamin & Zschokke, 2003). Nesticids are mostly found in caves. Among nesticid spiders collected during an expedition to the island of Sumba by the Naturhistorisches Museum, Basel, two adult specimens of an undescribed species were discovered. This new species has long legs, is pale and lack eyes, typical morphological adaptations for life in caves. Details of the expedition and a description of the locality are given in Bühler & Sutter (1951).

MATERIAL AND METHODS

Morphological structures were examined on temporary mounts embedded in glycerin. All drawings were made with a Nikon Labophot-2 and a Nikon SMZ-U microscope with drawing tube. The methods are described in detail in Benjamin (2000) and in Benjamin & Jocqué (2000). Measurements are in mm. All specimens examined are deposited in the Naturhistorisches Museum, Basel, NMB. Terminology of male palpal sclerite follows Lehtinen & Saaristo (1980) and Coddington (1990).

TAXONOMY

Nesticella marapu sp. n.

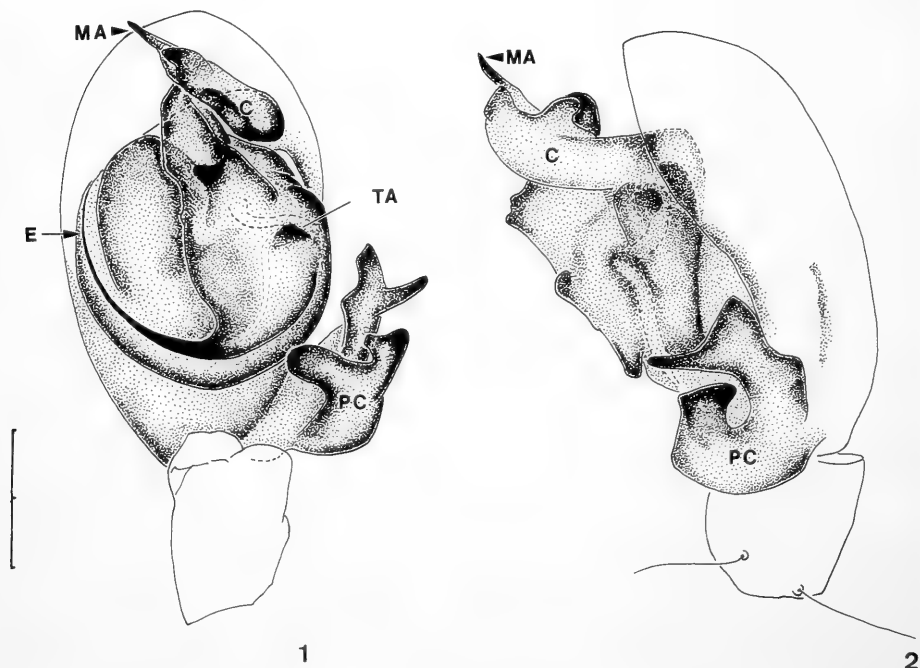
Figs 1-5

Types: ♂ holotype (NMB 2751a) and ♀ paratype (NMB 2751b), Indonesia, Sumba, Weimangura, Marro Cave, 440m, 25.08.1949, leg. Alfred Bühler and Ernst Sutter.

Etymology: The specific name is derived from Marapu, meaning spirits of ancestors. The main aim of the traditional Sumbanese religion is to maintain a peaceful and fruitful relationship with Marapu. Used as a noun in apposition.

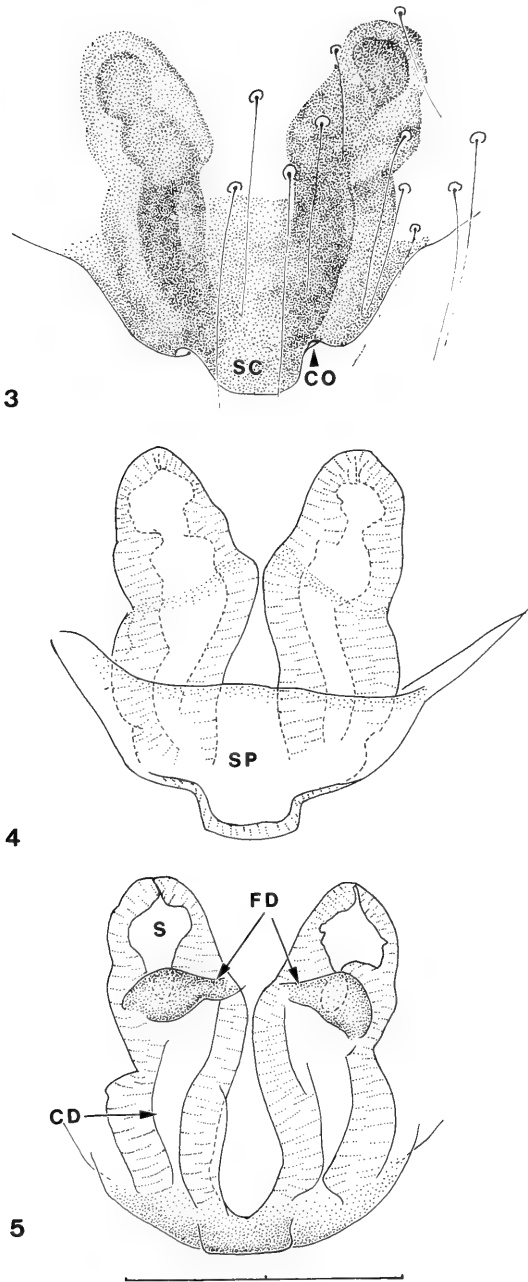
Diagnosis: *Nesticella marapu* sp. n. can be distinguished from all *Nesticella* species by the beak-shaped paracymbium and by the shape of the conductor.

Description: MALE (holotype). Colouration pale yellow. Carapace flattened, covered with some erect setae, mostly confined to the cephalic area. Eyes absent, no traces of eye sockets visible. Sternum covered with erect setae. Chelicerae without teeth, fangs reddish. Legs densely covered with thin long setae. Abdomen with some faint grey markings, covered with erect setae. Colulus very small, much smaller than that of the female, two erect setae present. Palpal paracymbium (PC) bifurcate, beak-shaped, both branches with distal modifications (Figs 1-2). Median apophysis (MA) tapering to a point. Tegular apophysis (TA) present in the form of a blunt elevation (Fig. 1; corresponding to "tegular apophysis 1" in Lehtinen & Saaristo (1980) and "theridiid tegular apophysis" of Coddington (1990)).



FIGS 1-2

Nesticella marapu sp. n. 1. Left male palp, ventral view. 2. Ditto, retrolateral view. C conductor; E embolus; MA median apophysis; PC paracymbium; TA tegular apophysis. Scale line: 0.2 mm.



FIGS 3-5

Nesticella marapu sp. n. 3. Epigynum, ventral view. 4. Vulva, ventral view. 5. Ditto, dorsal view. CD copulatory duct; CO copulatory opening; FD fertilization duct; S spermatheca; SC scape; SP sclerotised plate. Scale line: 0.2 mm.

Measurements: total length 2.3; carapace length 1.2; carapace width 1.1. Legs:

	I	II	III	IV
femur	2.8	1.7	1.3	2.0
patella	0.4	0.4	0.4	0.4
tibia	2.5	2.2	1.8	2.3
metatarsus	2.4	1.0	0.6	1.7
tarsus	1.0	0.9	0.5	0.8
total	9.1	6.2	4.6	7.2

FEMALE. Carapace bright yellow, flattened, covered with erect setae. Eyes absent, no traces of eye sockets visible. Sternum bright yellow, with many erect setae. Chelicerae yellow with three reddish teeth on promargin of the groove, fangs reddish, sickle-shaped. Legs pale yellow, slender, densely covered with long setae. Palp with a long, sickle-shaped claw. Abdomen pale yellow with diffuse grey markings, covered with erect red-brown setae. Colulus large, with two setae on ventral surface.

Epigynum with a square scape projecting outwards (SC in Fig. 3) and extending into a thin sclerotized plate beyond the scape (SP in Fig. 4). Copulatory openings (CO) originating at lateral sides of the scape. Copulatory ducts (CD) leading inwards to the spermathecae (S). Fertilization ducts (FD) as in Fig. 5.

Measurements: total length 2.6; carapace length 1.2; carapace width 1.0. Legs:

	I	II	III	IV
femur	2.0	1.7	1.3	2.0
patella	0.3	0.3	0.3	0.3
tibia	1.7	1.0	1.0	1.8
metatarsus	2.2	1.5	1.0	1.8
tarsus	0.8	0.7	0.7	0.7
total	7.0	5.2	4.3	6.6

Distribution: Known only from the type locality. The Marro cave is about 3 km long and situated close to Kabalidana, west of Waimangura (Bühler & Sutter, 1951).

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***Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva**

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***Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva.** - According to field observations performed in 2002 and 2003, the amphipod species *Dikerogammarus villosus* (Sowinsky, 1894) is now well established in Lake Geneva. The author predicts that this and future invasions by *D. villosus* will have serious effects on freshwater ecosystems.

Key-words: *Dikerogammarus villosus* - amphipod - biological invasion - ecological impact.

INTRODUCTION

The Ponto-Caspian amphipod (crustacean) *Dikerogammarus villosus* (Sowinsky, 1894) is currently among the most successful invaders of aquatic ecosystems in Europe (Dick & Platvoet, 2000; Bij de Vaate *et al.*, 2002). Being a native of the Ponto-Caspian Region, this species is widely distributed in the Black Sea, Azov Sea and Caspian Sea basins, from the lower reaches and delta of the Danube River to the Volga River (Carausu *et al.*, 1955). After invading the Danube in Austria in 1989, *D. villosus* was collected for the first time in the upper reaches of the river Danube in 1992 (Neseman *et al.*, 1995). In 1994 the species was recorded in the lower Rhine River (Bij de Vaate & Klink, 1995). Two years later *D. villosus* was discovered in the Moselle River and in 1997 for the first time in the French hydrosystem in the Saone River (Devin *et al.*, 2001; Bollache, 2003). In 1998 it was recorded in the Rhone River and in the Meuse River. Two years later *D. villosus* was detected in the Seine River (in 2000) and three years later in the Loire River (in 2001). Field surveys and laboratory experiments indicate that the ecological impact of a *D. villosus* invasion may be severe (Van der Velde *et al.*, 2000). For example, Dick and Platvoet (2000) have shown in Netherland freshwaters that *D. villosus* was rapidly eliminating *Gammarus duebeni* (Lilljeborg, 1851) and *Gammarus tigrinus* (Sexton, 1939), respectively, a native and an invader species from North America. In addition, *D. villosus*, being larger than the other freshwater amphipod species in western Europe, is known to prey on numerous macroinvertebrates (Dick *et al.*, 2002), and an isotope analysis ($\delta^{15}\text{N}$) indicated that it

is active at the same trophic level as fish species (Marguillier, 1998). My study, based on field observations in 2002 and 2003, demonstrates that *D. villosus* is now established in Lake Geneva.

MATERIAL AND METHODS

Four sites in France were sampled (Fig. 1). Yvoire, Corzent, Thonon-les-Bains and Lugrin. Gammarids were collected by kick-sampling using a hand net. *D. villosus* was identified by using the key of Carausu *et al.* (1955). Only adult individuals were

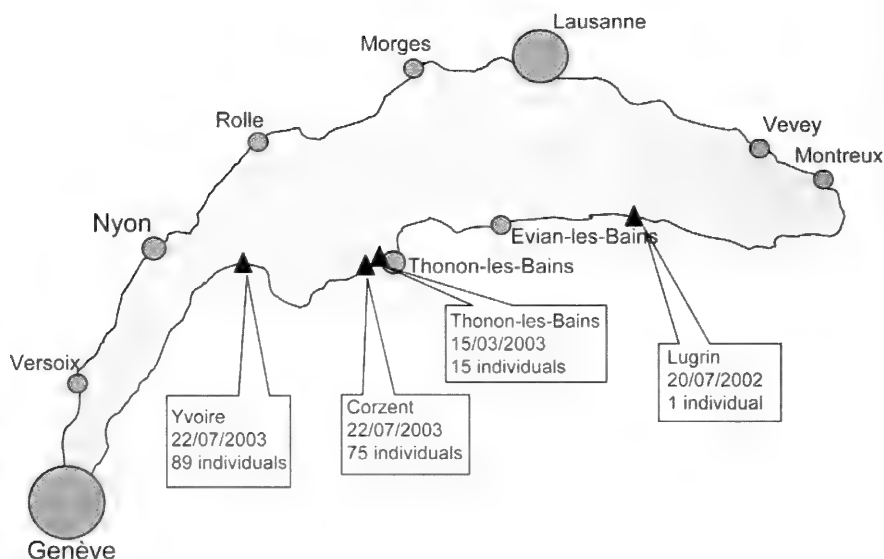


FIG. 1

Map of Lake Geneva with sampling sites (full triangles), and number of *D. villosus* specimens collected at each site on certain dates.

examined, as most of the species-specific diagnostic characters are fully developed and more obvious in these specimens. *Dikerogammarus* can easily be separated from *Gammarus* by the striking difference in the morphology of their third uropods. In the genus *Gammarus* the inner and outer rami are well developed, with the inner ramus varying from 1/3 to 3/5 of the length of the outer ramus (Fig. 2a), while in the genus *Dikerogammarus* the inner rami are vestigial (Fig. 2b). *D. villosus* males and females bear two protuberances with spines on the back of the first and second urosome (see fig. 3), and short setae on the peduncle of the second antennae. Moreover there is strong sexual dimorphism in the flagellum of the second antennae, which is distally much more densely setose in males than in females (Fig. 2c). Long and dense setae are also present on the first and second gnathopods of males (Fig. 2d).

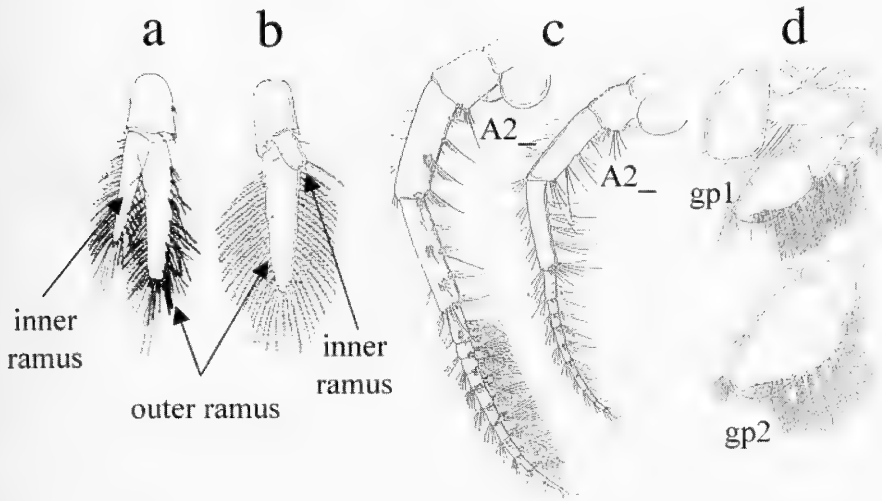


FIG. 2

(a) *Gammarus pulex*, third uropod after Roux, 1967; (b) *Dikerogammarus villosus*, third uropod after Carausu *et al.*, 1955; (c) *D. villosus* male and female, second antenna after Carausu *et al.*, 1955; (d) *D. villosus* male, first and second gnathopods after Carausu *et al.*, 1955.

RESULTS

D. villosus was observed for the first time in Lake Geneva during the summer of 2002 at Lugrin (France); one specimen was found among specimens of the native gammarid, *Gammarus fossarum*. In 2003 *D. villosus* was recorded at the other three French sites prospected, Yvoire harbour, Thonon-les-Bains (INRA station) and Concert harbour (Fig. 3), without any other gammarid species present and was found to be very abundant in rockpools and under porous stones, hanging on tightly to the bumps on the stones.

DISCUSSION

The present and previous data allow us to attribute the arrival of *D. villosus* to Lake Geneva between the years 2001 and 2002. The reason for this recent massive invasion of a Ponto-Caspian species in central and western Europe is the increasing ionic content of large European rivers in the last decades, caused by industrial and agricultural pollution (Jazdzewski & Konopacka, 2002). Another cause is explained in the "invasional meltdown hypothesis" (Ricciardi & Rasmussen, 1998; Simberloff & Von Holle, 1999; Ricciardi, 2001) according to which a previously invasion of the zebra mussel *Dreissena polymorpha* (Pallas, 1771) in the central and western European freshwater ecosystem may have facilitated the invasion of *D. villosus* by providing substrate, food and shelters. The same scenario is invoked to explain the establishment and dispersal of *Chaetogammaris ischnus* (Stebbing, 1906) another Ponto-Caspian amphipod, in the Great Lakes of North America (Witt *et al.*, 1997; Dermott *et al.*, 1998;

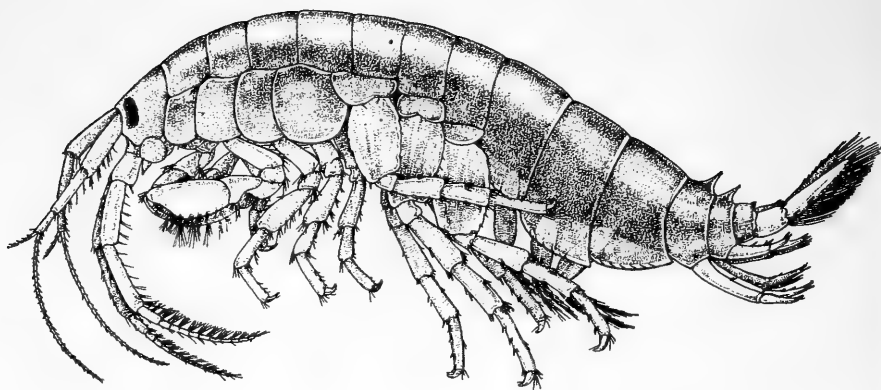


FIG. 3

Dikerogammarus villosus adult male after Carausu *et al.*, 1955, modified after Bollache, 2003.

Nalepa *et al.*, 2001). Dick *et al.* (2002) have recently shown in the Netherlands that predation by the invader *D. villosus* was significantly greater than predation by the native amphipod species *G. duebeni*. The predatory capacity of *D. villosus*, together with its high ability to disperse by anthropogenic means, lead I to predict that *D. villosus* will soon be present in the others lakes of Switzerland, and that this poses a serious threat for the biodiversity of freshwater ecosystems in Europe.

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Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae

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Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. - This paper reviews the European Hydrozoa species belonging to the families Oceanidae and Pachycordylidae. Emended diagnoses for the Oceanidae, the Pachycordylidae, and for some of their genera are provided. Due to the paucity of suitable characters, the macrotaxonomy of the two families is unsettled and must be regarded as provisional. The family Oceanidae includes the genera *Cordylophora*, *Corydendrium*, *Merona*, *Oceania*, *Rhizogeton*, *Turritopsis*, *Turritopsoides*, and the new genus *Similomerona* gen. n. The family Pachycordylidae includes the genera *Pachycordyle* and *Silhouetta*. *Turritopsis polycirra* and *T. dohrnii* are both regarded as valid species and distinct from *T. nutricula* of the western Atlantic. Histological sections confirmed that *Turritopsis polycirra* is hermaphroditic and larviparous, while *T. nutricula* is dioecious and oviparous. *Turritopsis rubra* (Farquhar, 1895) comb. n. from New Zealand is also regarded as a valid species and removed from synonymy with *T. nutricula*. The known distribution of *Corydendrium dispar* is extended to include the Faroe Islands. A former record of *C. dispar* from Denmark is referred to *Pachycordyle navis* (Millard, 1959) comb. n. *Pachycordyle fusca* Müller, 1913 is regarded as a likely synonym of *Pachycordyle pusilla* (Motz-Kossowska, 1905) comb. n.

Key-words: Marine invertebrates - Cnidaria - Hydrozoa - Antoathecata - Oceanidae - Pachycordylidae - Clavidae - descriptions - revision - taxonomy.

INTRODUCTION

Although the athecate hydroids and anthomedusae of the European coasts have a long taxonomic history, with some species going back to Linnaeus, we lack a comprehensive, up-to-date treatise like the one by Cornelius (1995) for the thecate hydroids of North-West Europe. Some groups are covered by good monographs. The Stylasteridae have been monographed by Zibrowius & Cairns (1992). The European *Hydra* species are treated by Holstein (1995). The monograph of Brinckmann-Voss

(1970) covers the Capitata, but is restricted to the Mediterranean fauna only. Naumov's (1969) book on the Hydrozoa of the USSR includes also the Baltic Sea, but its scope is not European for the most part. Russell's (1953) work on the British medusae is certainly still very valuable, but treats only species with a medusa phase. There are also some recent worldwide reviews of single families which also include European species, e. g. by Segonzac & Vervoort (1995) for the genus *Candelabrum*, Boero *et al.* (2000) for *Zanclea*, or Schuchert (2001b) for the Corynidae. Some similar, older publications, e. g. Vannucci & Rees (1961), Rees (1962), also offer much valuable information. However, the scattered information makes it desirable to review all species. The author therefore aims at bringing together in a series of publications all important taxonomic information on the European Anthoathecata.

All European species belonging to the order Anthoathecata (Cornelius, 1995) will be revised, as will the supraspecific taxa where necessary. Taxa for which there exist recent revisions will, however, not be treated in detail. Wherever possible, taxa will be redefined so that most of them are plausibly monophyletic. However, these animals offer only few morphological characters and they tend to be insufficiently complex. Many shared characters are thus very prone to be homoplasies. A comprehensive phylogenetic analysis based exclusively on morphology was therefore considered unreliable and only a few suitable characters could be used to delimit some genera and families.

The geographic region covered in this revision reaches from the North Cape to the Canary Islands and the European parts of the Mediterranean. It excludes the Azores and Iceland. The hydroid species of the Azores are listed in Rees & White (1966) and Cornelius (1992). The hydroid fauna of Iceland has recently been reviewed by Schuchert (2001a).

In the present paper, the families Oceanidae and Pachycordylidae have been revised. The macrotaxonomy of both families, as well as their genera, is particularly unsettled and disputed. It can therefore only be regarded as provisional.

MATERIAL AND METHODS

Standard histological techniques were used to obtain serial thin sections. Animals fixed in formaldehyde were embedded in paraffin and serial sections of 8-10 μm thickness were made. Staining was with Hematoxylin and Eosin. All slides have been deposited in the MHNG.

ABBREVIATIONS

BMNH	The Natural History Museum, London, England
ICZN	International Code of Zoological Nomenclature, 4 th Edition
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
RMNH	Naturalis, Leiden, The Netherlands
ZMUC	Zoological Museum Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany

TAXONOMIC PART

OCEANIDAE Eschscholtz, 1829

SYNONYMS – Cordylophoridae von Lendenfeld, 1885.

DIAGNOSIS – Anthoathecata Filifera with monomorphic or polymorphic polyps. Gastrozooids bearing filiform tentacles scattered over at least distal third of hydranth body, not concentrated in a narrow band. Gonophores developing either below the hydranth body, or directly on stolons, or from stolonal blastostyles with perisarc-covered pedicels. Gonophores either free medusae or fixed sporosacs. Free medusa, where present, with four mouth lips, mouth margin fringed with numerous spherical nematocyst clusters; four simple radial canals, without centripetal canals, juveniles with four or more tentacles, adults with numerous tentacles, these not grouped, their nematocysts evenly distributed. Ocelli present on adaxial bases of tentacles. Gonads on interradial walls of manubrium.

REMARKS – The name Oceanidae Eschscholtz, 1829 is here revived and it replaces the junior synonym Cordylophoridae von Lendenfeld, 1885 as well as the name traditionally used for the present group: Clavidae McCrady, 1859.

If the genus *Oceania* Péron & Lesueur, 1810 is regarded as valid, then automatically also the family name Oceanidae Eschscholtz, 1829 becomes available. If the genera *Oceania* and *Cordylophora* are placed within the same family, then *Oceania* is a senior synonym of Cordylophoridae von Lendenfeld, 1885. The latter name was recently re-introduced by myself (Schuchert 2001a, 2003a, 2003b) without being aware of the name Oceanidae Eschscholtz, 1829.

The scope of the family Oceanidae as used here corresponds largely to what was until recently known as Clavidae (comp. Millard, 1975; Bouillon, 1985; Calder, 1988a; Schuchert, 1996; Bouillon & Boero, 2000). The possession of scattered filiform tentacles was usually considered a diagnostic trait of the family Clavidae. However, also other filiferan families, like the Pandeidae or Hydractiniidae, have polyps with scattered tentacles. The hydroid of *Stomotoca atra* L. Agassiz, 1862, a member of the family Pandeidae, has scattered filiform tentacles (Boero & Bouillon, 1989) and in the absence of information on the medusa phase would certainly have been classified among the former Clavidae. Scattered tentacles are also prevalent in the sister group of the Filifera, the Capitata (see Petersen, 1990 for diagnoses for both taxa). The character “scattered filiform tentacles” must thus be used with necessary caution, although it is potentially a synapomorphy for the family Oceanidae. The isolated occurrences of scattered filiform tentacles in the Pandeidae and Hydractiniidae must then be explained as homoplasies.

The genus *Clava* does not belong to the Oceanidae. Schuchert (2001a) showed that the genus *Clava* Gmelin, 1791 must be transferred to the family Hydractiniidae. Although *Clava multicornis* (Forsskål, 1775), the type species of *Clava*, has scattered tentacles similar to many Oceanidae, its gonophores develop on the hydranth body directly below the tentacles. This gonophore position is the plesiomorphic condition within the Anthoathecata and it is found in filiferan families such as the Hydractiniidae and Eudendriidae, as well as in many other hydroids, e. g. Corynidae, most Zancleidae, some Limnomedusae, and some Leptothecata lacking a gonotheca. In some Filifera,

however, the site of gonophore development has been shifted towards proximal, either to the hydranth pedicels, branches, or even stolons. This downward shift is an apomorphy found in the Oceanidae, Bougainvilliidae, Pandeidae, Cytaeididae and some other minor groups. In the Calycopsidae, the site of the gonophores is somewhat unclear because they are produced at the insertion of the naked pedicel with the hydranth body (comp. Brickmann-Voss, 1979; Schuchert, 1996).

Because the genus *Clava* shows the plesiomorphic condition of gonophore position, and because there are no evident synapomorphies, it cannot be included in the Oceanidae as defined here. *Clava* is better transferred to the Hydractiniidae. Some Hydractiniidae have similarly scattered filiform tentacles (comp. Millard, 1975; Schuchert, 1996; Bouillon *et al.* 1997) and there are actually no significant morphological differences that would distinguish *Clava multicornis* from the Hydractiniidae, particularly when compared to *Clavactinia*. The similarity of *Clava* with the Hydractiniidae has also been noted by Boero *et al.* (1998), but they regarded it as distinct on account of its monomorphic polyps. This is, however, not convincing as also several hydractiniids lack a polymorphism and gonophores develop on gastrozooids that remain otherwise unchanged (e. g. *Hydractinia sarsii*; see Schuchert, 2001a). Gonophore producing hydranths generally reduce their size and tentacle numbers, an effect named reproductive exhaustion. This reproductive exhaustion should not be confounded with a true, pre-determined polymorphism, in which gonozooids differ from gastrozooids even before they develop gonophores.

Because *Clava*, the genus to which Clavidae is anchored, must be transferred to the Hydractiniidae, the taxon name Clavidae is not available anymore for the remaining genera of this family (Clavidae actually becomes a senior synonym of Hydractiniidae, see Schuchert 2001a). The name Oceanidae is therefore proposed for these remaining genera.

The original scope of Oceanidae Eschscholtz, 1829 was very broad and encompassed genera now allocated to several families. This is certainly due to the original broad meaning of the genus *Oceania*, but this should not be seen as an argument against its usage. Many other old hydrozoan names that are still in use have a similar history (e. g. the Linnean genera *Tubularia* and *Sertularia*). The family Oceanidae is tied to the genus *Oceania* and applies to the family that contains this genus, irrespective of the original scope of the family. The historical usage of *Oceania* is summarized under remarks for the genus *Oceania*.

The family Oceanidae thus comprises the following previously known genera: *Cordylophora*, *Corydendrium*, *Merona*, *Oceania*, *Rhizogeton*, *Turritopsis*, and *Turritopsoidea*. Additionally, the new genus *Similomerona* is proposed.

The family Oceanidae as defined here lacks a clear synapomorphy, hence its delimitation from other families like the Bougainvilliidae and Calycopsidae is not strict (Millard, 1975; Calder, 1988a expressed similar thoughts). It is possible that the family Oceanidae is not a monophyletic group and future results of sequence phylogenies might require a regrouping. The taxonomy of the Oceanidae must thus be regarded as provisional only.

It was necessary to re-define some of the genera included in this family, both to accommodate some recently described species which do not entirely fit formerly

provided diagnoses and to use as much phylogenetic information as possible to delimit monophyletic groups. Nearly all species described as belonging to these genera were considered for the diagnoses, although not all are discussed here. Unfortunately, the available synapomorphies are very limited and I failed to produce a convincing phylogenetic analysis. The genera were therefore delimited in a way that minimizes name changes and maximizes to some degree the possible monophyly. The synapomorphies and some important problems of the genera are discussed in the following sections.

Considering only the life-cycle, species with a medusa phase like *Turritopsis nutricula* or *Oceania armata* must represent the least derived condition because a medusa was present in the ground plan of the Anthoathecata (see Petersen, 1990; Schuchert, 1993; Boero *et al.*, 1998).

The current usage of *Turritopsis* is unmistakable and the genus is well delimited. The vacuolated gastrodermal cells forming a peduncle on top of the manubrium represents a clear apomorphy.

The genus *Oceania*, although in current usage quite well defined, poses taxonomic problems. They are outlined under remarks for the genus. *Oceania* auct. is only gradually different from *Turritopsis* and both genera should perhaps be merged, as it has been done by Haeckel (1879). Also McCrady (1857) thought that *Turritopsis* is very closely related to *Oceania* auct., and he initially considered *Turritopsis* to be only a subgenus of *Oceania*. To maintain nomenclatural stability, both genera are here employed. Traditionally, *Turritopsis* was kept separate from *Oceania* auct. on account of its manubrial peduncle formed by vacuolated cells (Mayer, 1910; Kramp, 1961). *Oceania* has a gelatinous peduncle, but the most proximal parts of the radial canals are also dilated and composed of large cells, exactly as in *Turritopsis*. In *Oceania* and in large *Turritopsis* medusae, these vacuolated cells are continued along the manubrium as four perradial ribs, resembling claws that clasp the manubrium (Figs 2C, 3B, 5). The vacuolated cells and the radial ribs could be a synapomorphy of the two genera. *Oceania* differs from *Turritopsis* in having stalked nematocyst clusters along its mouth, while they are without a distinct stalk in *Turritopsis*. Adult *Turritopsis* and *Oceania* medusae also resemble medusae of the family Pandeidae (comp. Kramp, 1959), but the lining of the mouth margin with nematocysts clusters separates them from the latter family (see Fig. 5C). These nematocyst clusters are, however, not a unique synapomorphy, as also at least some medusae of the family Calycopsidae have them (see e. g. *Bythotiara* spec. in Schuchert, 1996: fig. 9e). Medusae of the family Calycopsidae are, however, easily separable on account of their tentacle morphology.

Corydendrium parasiticum, type species of its genus, has gastrodermal gonads developing within the perisarc tubes of the hydranth pedicels and they are only extruded when mature. This is a clear apomorphy. The same internal gonads are also found in *Corydendrium brevicaulis* Hirohito, 1988, although this species forms variably either branched or stolonal colonies. *Corydendrium parasiticum* possesses another apomorphy: the side-branches remain within the perisarc tube of the original branch and they emerge only after a certain distance (Weismann, 1883). The perisarc of the side-branch is already formed within the tube of the original branch, leading to a typical nested structure of the perisarc tubes, best seen in cross-sections (well visible even in hand-made sections). This clear apomorphy is also found in *Corydendrium*

dispar Kramp, 1935 (see Kramp, 1935: fig. 2). However, *C. dispar* has external gonophores, although the structure of the male ones resemble that of *C. parasiticum*. *Turritopsis nutricula* hydroids also form erect, branching colonies with adnate side-branches. The perisarc tubes of *Turritopsis*, however, are not nested. This was verified in hand-made cross-sections of colonies from the Mediterranean and the Andaman Sea. The adnate side branches of *T. nutricula* represent perhaps only the first steps of a development that lead to the nested tubes seen in *Corydendrium parasiticum*. Because *Turritopsis* does not possess any of the two apomorphies found in *Corydendrium*, Kramp's (1935) proposal of merging *Turritopsis* and *Corydendrium* is here not adopted. This would also cause very troublesome name changes.

Merona has very obvious apomorphies: the nematophores in perisarc tubes and the sporosacs on blastostyles. The genus thus corresponds very likely to a clade. Antsulevich & Polteva (1986) described a new *Merona* species from the Kurile Islands which they named *Merona nematophorum*. It has naked nematophores resembling modified hydranths and it produces sporosacs issuing directly from the stolons. These combined differences suggest that *M. nematophorum* has perhaps attained its superficial similarity to other *Merona* species by convergence. Unfortunately, all these animals offer too few morphological characters to substantiate this with the aid of a reliable phylogenetic analysis and we have to wait for a molecular phylogenetic investigation. Meanwhile, it seems appropriate to follow Calder's (1988a) opinion that *M. nematophorum* should be transferred to a new genus. Therefore, the new genus *Similomerona* proposed.

The diagnosis for *Similomerona* **gen. n.** is as follows: "Anthoathecata Filifera with polymorphic polyps; feeding zooids stolonial, with scattered filiform tentacles; defensive zooids with rudimentary tentacles, not in perisarc tubes; gonophores sporosac developing on stolons." Type species is *Merona nematophorum* Antsulevich & Polteva, 1986. The species name will thus become *Similomerona nematophorum* (Antsulevich & Polteva, 1986) **comb. n.** The genus is currently monotypic. It is not represented in the European fauna.

Rhizogeton, with its sporosacs on the stolons and the stolonial or sessile hydranths, is easily distinguished from other members of the family. Both characters are apomorphies, but they are not independent and the *Rhizogeton*-like morphology can be imagined to have easily originated from various other genera. It is thus very prone to be polyphyletic.

Turritopsoides brehmeri Calder, 1988b, the type species of the genus, normally forms purely stolonial colonies, but infrequently some shoots bear a side-branch. These side-branches are adnate to the branch of origin, an apomorphy also found in *Turritopsis nutricula*. This, and the branched spadix of the female sporosacs, justify keeping the genus separate from *Rhizogeton*. The genus *Turritopsoides* is not represented in the European fauna.

The genus *Cordylophora* is difficult to define in terms of evident apomorphies, and the delimitation to *Pachycordyle*, here placed in a separate family, is based primarily on the tentacle arrangement of the hydroids (for an opposing view see Morri, 1980; or Stepanjants *et al.*, 2000). In the Pachycordylidae, the tentacles are confined to a small band below the hypostome, while in the Oceanidae they are more scattered.

Some genera that have at times been assigned to the Clavidae sensu Bouillon (1985) are either invalid or do not belong to the Oceanidae as defined here:

Campaniclava Allman, 1864: referred to the Pandeidae (Picard, 1956).

Clava Gmelin, 1791: see above and Schuchert (2001a), referred to Hydractiniidae.

Cnidostoma Vanhöffen, 1911: this genus was referred to the Clavidae sensu Bouillon, 1985 by Picard (Picard in Kramp, 1961: 444), a proposal accepted by Bouillon (1985). Kramp (1959, 1961) allocated it to the Cytaeididae. Examination of *Cnidostoma fallax* from the Ivory Coast (MHNG INVE 27133) confirmed the accurate description of Vanhöffen (1911). The overall habit, but especially the manubrium ending in four clusters of stalked nematocytes, bring this species very close to medusae of the Hydractiniidae and *Cnidostoma* is here provisionally allocated to that family.

Hataia Hirai & Yamada, 1965 is excluded from the Oceanidae because its sole species (*Hataia parva*) possesses stenoteles and must thus be transferred to the Capitata (see Yamada & Kubota, 1991).

Tubiclava Allman, 1863: Allman (1872: 256) wrote: "...since I do not at this distance of time feel absolutely certain as to the identity of the Dublin Bay and Torquay hydroids, the gonosome of *Tubiclava* must still be regarded as in some respects hypothetical, and the genus itself as defined above must be accepted with just so much of a provisional element." The type species of the genus *Tubiclava* is *T. lucerna* (by monotypy). Allman (1863, 1872) described *Tubiclava lucerna* based on infertile material. He thought that he had observed similar colonies a few years earlier that had gonophores, but which he previously thought to be an aberrant *Clava multicornis*. Rees (1956: 505) maintained that *Tubiclava lucerna* is a problematic species and he doubted whether Allman had actually observed sporosacs. *Tubiclava* is a doubtful genus and should therefore not be used anymore. Although occasionally other authors mention findings of *Tubiclava lucerna*, this species remains doubtful and no material could be located in any museum. All other species allocated to *Tubiclava* are either not recognizable or must be referred to other genera. *Tubiclava fruticosa* Allman, 1872 was based on infertile material and is not recognizable. Picard (1958: 189), referred all Mediterranean records of *T. fruticosa* to *Pachycordyle napolitana*, but some in Riedl (1959) are evidently *Turritopsis dohrnii*. Also *Tubiclava rubra* Farquhar, 1895 belongs to the genus *Turritopsis* (see Schuchert, 1996). *Tubiclava laxa* Fraser, 1938 must be referred to the genus *Merona*, while *Tubiclava triserialis* Fraser, 1938 is not recognizable. In his diagnosis of *Tubiclava* Allman (1872) stated that the sporosacs develop on the hydranth body immediately below the tentacles, just as in *Clava multicornis*. This renders the genus incompatible with the concept of the Oceanidae as used here. The theoretical genus *Tubiclava* sensu Allman has some resemblance to *Millardiana* Wedler & Larson, 1986. *Millardiana longitentaculata* Wedler & Larson, 1986, presently the only species of its genus, is not known from the region under investigation, but Cornelius (1992) reported it from the Azores and it is conceivable that this species could also be found along the coasts of southern Europe.

Millardiana Wedler & Larson, 1986 has sporosacs on the hydranth body. Therefore, using the same arguments as given above for *Clava*, it can neither be included in the Oceanidae nor the Bougainvilliidae as proposed by Calder (1988a). At present, the affinities of *Millardiana* are unclear. It should preferably be placed in a new family.

Pachycordyle Weismann, 1883: this genus is here placed in a separate family, the Pachycordylidae. For more details see under remarks for this family (includes also *Thielia* Stepanjants *et al.*, 2000).

Rhizodendrium Calder, 1988a: it might be necessary to use this genus for some stolonial Oceanidae to separate them from *Rhizogeton fusiformis* L. Agassiz, 1862 (type species of the genus). It is not used here because we do not yet know the gonophores of the type species of *Rhizodendrium* (see under genus *Rhizogeton*).

The order of the genera given below has no phylogenetic meaning. It merely attempts to group resembling genera to facilitate comparisons.

***Turritopsis* McCrady, 1857**

SYNONYMS – *Clavula* Wright, 1859; *Dendroclava* Weismann, 1883.

TYPE SPECIES – *Turritopsis nutricula* McCrady, 1857.

DIAGNOSIS – Erect, branching hydroid colonies, side-branches and hydranth pedicels adnate to for some distance, perisarc tubes not nested. Hydranths spindle- to club-shaped; filiform tentacles scattered over much of hydranth body. Gonophores develop on the hydrocauli in perisarc covered region and are liberated as medusae. Medusae with proximal portion of radial canals swollen through vacuolated gastrodermal cells, forming a peduncle-like mass on top of manubrium, in larger animals continued on manubrium as perradial ribs. Tentacles numerous and evenly distributed. Mouth four-lipped, fringed with numerous spherical nematocyst clusters, these without distinct stalk. Ocelli adaxial, at tentacle base.

REMARKS – For the taxonomic history of this genus see Calder (1988a). For the publication date of McCrady's works see Calder *et al.* (1992).

Large *Turritopsis* and *Oceania* medusae resemble each other quite closely. Both have large cells at the proximal end of their radial canals which are continued along the manubrium as four perradial ribs, resembling claws that clasp the manubrium (Figs 2C, 3B, 5). *Oceania* differs from *Turritopsis* in having stalked nematocyst clusters along its mouth, while they are without a distinct stalk in *Turritopsis*. In addition, the manubrium base of *Oceania armata* is somewhat constricted. This allows to distinguish even badly preserved material (Kramp, 1965).

***Turritopsis polycirrho* (Keferstein, 1862)**

Figs 1 & 2C-D

? *Medusa sanguinolenta* Modeer, 1791: 26.

? *Cyanea coccinea* Davis, 1841: 236, pl. 2 figs 1-3.

? *Oceania globulosa* Forbes, 1848: 29, pl. 3 fig. 3.

Turris neglecta – Wright, 1859: 106; Hincks, 1868: 13, pl. 3 fig. 1.
[not *Turris neglecta* Lesson, 1843].

Clavula Gossii Wright, 1859: 106, pl. 8 fig. 1.

Oceania polycirrho Keferstein, 1862: 26, pl. 2 figs 11-13.

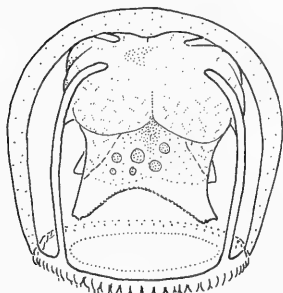


FIG. 1

Turritopsis polycirrho (Keferstein, 1862), sketch after preserved material from The Netherlands, note that the radial canals overtop the mass of vacuolated cells, a few eggs are visible on the lower part of the manubrium, tentacles are lost, scale equals 1 mm.

? *Tubiclava fruticosa* Allman, 1872: 257, pl. 2 figs 5-6.

Turritopsis polynema Haeckel, 1879: 66, new name.

Turritopsis polycirrho – Hartlaub, 1897: 480, pl. 16c fig 2; Hartlaub, 1911: 202, figs 179-180.

Turritopsis nutricula – Kramp, 1930: 13, map 5; Russell, 1953: 115, figs 54A-C, 55, 56, pl. 5 figs 1-5, pl. 29.

[not *Turritopsis nutricula* McCrady, 1857].

MATERIAL OF *T. POLYCIARRHA* – ZMUC, as *T. nutricula*, North Sea, 50° 59' N 1° 37' 5 E, collected 23 August 1904, about 5 medusae, some with planulae, bells not so well preserved, one used for serial sectioning, deposited as MHNG INVE 33967 – RMNH Coel 10345, as *T. nutricula*, Texel, The Netherlands, North Sea, coll. 1973; 19 medusae, 18 clearly with oocytes or embryos, two specimens with visible oocytes were used to make serial sections, deposited as MHNG INVE 34417 and 34418 – IRSNB, hydroids as *T. nutricula*, coll. J. Bouillon June 1964 Roscoff, 2 lots, one small colony on microscopic slide, overgrowth of *Fosliella farinosa* indicates that it has been cultivated for quite some time; the second lot is a small polyp with gonophores growing on a piece of an unidentified gelatinous animal.

MATERIAL OF *T. NUTRICULA* FOR COMPARISONS – ZMUC, Beaufort Inlet, North Carolina, USA, > 100 medusae, collected August to September 1962 and 1964 by J. Allwein, many mature animals, sexes clearly distinguishable, no brooding, 2 females and 2 males used for serial sections, deposited as MHNG INVE 33963 to 33966.

MATERIAL OF *T. RUBRA* FOR COMPARISONS – see also Schuchert (1996), as *T. nutricula* – About 50 living medusae collected around Rangitoto Island (Hauraki Gulf, New Zealand), July 2002, some deposited as MHNG INVE 33469, 2 males and 2 females used for serial sections (MHNG INVE 33968 to 33971).

TYPE MATERIAL – There presumably exists no type material of *T. polycirrho*.

DIAGNOSIS – Typical *Turritopsis* medusae, adults 4-5 mm in height and diameter, 80-90 tentacles, tentacle tips not inflated, umbrella top rounded, manubrium without gelatinous peduncle, on top of manubrium four blocks of vacuolated cells fused into a single compact mass, radial canals overtop this mass. Vacuolated cells continued downward on manubrium as bulging, perradial rib. Radial canals broad. Simultaneous hermaphrodites and larviparous. Colour: stomach and gonads brilliant red to dark crimson. Nematocysts of medusa (Russell, 1940): microbasic euryteles

(8-10) x (4) μm ; desmonemes (6-7) x (4-4.5) μm . Polyp phase inadequately known from nature, likely a stolonal or only sparingly branched colony, hydranths with scattered filiform tentacles, hydranth colour: red.

DESCRIPTION – See Russell (1953), who also provides good colour drawings.

BIOLOGY – Neritic species. Medusa present in autumn and winter months, occasionally until April; most abundant in September and October (Russell, 1953). Along the coast of The Netherlands, Van der Baan (1980) found it in December and January only. According to Kramp (1930), the medusae are presumably liberated from the hydroid during June or July. Teissier (1965) indicates August as the month of medusa liberation. Medusae present in the North Sea are considered to originate from the English Channel (Russell, 1953; Edwards, 1968).

DISTRIBUTION – English Channel; Great Britain, up to Firth of Forth in the east, up to Bristol Channel in the west; southern parts of the North Sea, sometimes as far east as Heligoland. Type locality: St. Vaast, Normandy, France.

COMPARISON OF REPRODUCTIVE STRATEGIES – The European *Turritopsis polycirra* and *T. dohrnii*, as well as other nominal *Turritopsis* species from the Pacific have been synonymized with the American *T. nutricula* (although McCrady (1857) did not mention where he had collected *T. nutricula*, it can be inferred from McCrady (1859) that Charleston Harbor must be the type locality). Particular attention was therefore paid to *Turritopsis* medusae from the east coast of the USA and they were compared to *Turritopsis* medusae from other regions. The morphology of more than 100 medusae originating from the USA were examined. They all matched the description of *T. nutricula* given by Mayer (1910) and Brooks (1886). Together with the proximity of the type locality, there is no doubt about their specific identification. Even cursory examination with a stereomicroscope reveals that the sexes must be separate as eggs are easily discernible in mature females. None of the females had larvae or developing embryos attached to the manubrium. Histological examination of two males and two females confirmed that individuals produced either sperms or eggs, but never both together (Figs. 2A-B). The spermatogenic cells are small cells with little cytoplasm and a strongly staining nucleus. They differentiate distally into spermatogonia and finally into spermatozoa (comp. Tardent, 1978). In clusters of mature or nearly mature sperms, their aligned tails become visible even under light microscopy by producing a filamentous structure. The American *T. nutricula* is thus clearly dioecious and oviparous. This has been noted by other authors as well (Brooks, 1886; Brooks & Rittenhouse, 1907).

About 24 *Turritopsis polycirra* medusae from the eastern Atlantic (North Sea) were obtained. No unambiguously identifiable males were found among them, but almost all specimens had eggs and some even had attached planulae. Due to the limited number of animals, only three medusae could be used for serial sectioning. The histological organization of the three proved to be clearly different from that observed in the American *T. nutricula*. Besides oocytes of all developmental stages, there often are pockets containing small cells with little cytoplasm that show differentiation into typical spermatozoa (Figs. 2C-D). Comparison with male *T. nutricula* from the USA

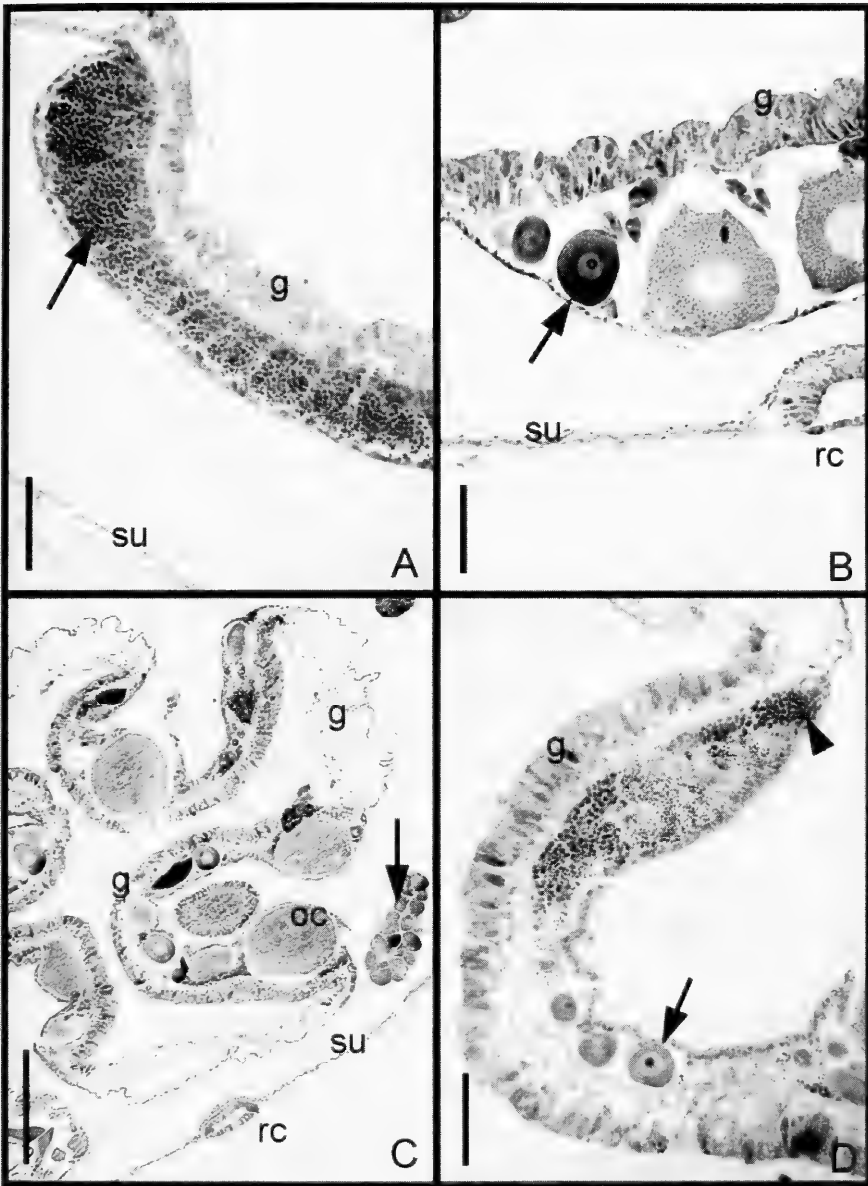


FIG. 2. Horizontal thin sections in region of gonads. A) Male *Turritopsis nutricula* medusa from the USA, arrow points to spermatogenic cells, scale equals 50 μm . B) Female *Turritopsis nutricula* medusa from the USA, arrow points to a developing oocyte, scale equals 50 μm . C) *Turritopsis polycirra*, mature hermaphroditic medusa from the North Sea, overview, arrow points to a developing embryo, the gonad contains oocytes as well as pockets of spermatogenic cells. Note the periradial vacuolated cells of the gastrodermis. Scale equals 20 μm . D) Higher magnification of animal depicted in C, arrowhead points towards spermatogenic cells, arrow points to an oocyte, scale equals 50 μm . Abbreviations: g = gastrodermis, oc = oocyte, rc = radial canal, su = subumbrellar musculature.

leaves no doubt that these must be spermatogenic cells as well as mature spermatozoa. The presence of eggs, developing embryos, and sperms in various stages of differentiation makes the European *T. polycirrha* a simultaneous hermaphrodite. This confirms similar observations by Hartlaub (1911), which, however, have largely been ignored. The fertilized eggs are brooded and released as fully formed planula larvae, a fact that has already been observed by several authors (Mayer, 1910; Russell, 1953).

Turritopsis medusae from New Zealand, until recently attributed to *T. nutricula* (see Schuchert, 1996), appear to be almost indistinguishable from *T. polycirrha* (Fig. 3A-B). Both have the same morphology and colour, and the same morphological arguments can be used to distinguish them from *T. nutricula* (table 1). However, in contrast to *T. polycirrha*, the New Zealandic *Turritopsis* is gonochoristic. Examination of more than 100 living, mature *Turritopsis* medusae from New Zealand (see also Schuchert, 1996) clearly showed that males and females can be distinguished using a stereomicroscope (10 x magnification). The females brood their larvae, sometimes even to the primary polyp stage (Fig. 3A-B; see also Schuchert, 1996). The examination of histological serial sections (2 females and 2 males) confirmed that the two sexes are clearly separate and that there are no differentiating sperm cells in the female medusae (results not shown). Because *Turritopsis* from New Zealand is thus distinct from both *T. nutricula* and *T. polycirrha*, it is preferable to regard it as a distinct species, namely *Turritopsis rubra* (Farquhar, 1895) new. comb.

TAXONOMIC HISTORY – Because the medusa of *T. polycirrha* is quite conspicuous due to its red colour, it was possibly mentioned by several early naturalists (see synonymy above and Russell, 1953) but it was Keferstein (1862) who gave the first reliable description. Due to the great similarity to the American *Turritopsis nutricula*, Mayer (1910) considered *T. polycirrha* to be only a synonym of the former. Kramp (1930) and Russell (1953) followed the arguments of Mayer, although Russell acknowledged the differences between the European and the American forms. Hartlaub (1911, 1917) and Browne (1916), both of whom presumably had seen living European material, did not agree and kept *T. polycirrha* separate from *T. nutricula*. Browne (1916: 179) kept both species distinct based on the following arguments:

T. nutricula: "... the radial canals, by a considerable thickening of their walls and coalescence, form a kind of endodermal peduncle upon which the stomach hangs."

T. polycirrha: "... a further development of the endoderm takes place, it is no longer confined to the walls of the radial canals, but grows across the top of the umbrella cavity and forms a homogenous mass of cells. This extension also grows downward and takes in the radial canals in the uppermost part of the subumbrella. The extension of the endoderm is recorded by the leaving of the outer half of the radial canal wall in situ alongside the umbrella. In adult specimens, the radial canals run alongside this mass of endoderm nearly to the top of the subumbrella and there they curve sharply inside to the stomach."

Browne's arguments translate into the observation that in *T. polycirrha* the four masses of vacuolated cells are completely fused and the outer portions of the radial

canals reach higher up and overtop the mass of vacuolated cells. The difference in the radial canals was also observed in the examined preserved material (comp. Figs 1 and 3D-E). In addition, the American *Turritopsis nutricula* has its mass of vacuolated cells more clearly split into four blocks, while in the European *T. polycirra*, the four blocks are tightly fused into one mass, although the fusion lines remain visible. Hartlaub (1917: 407) also noted this difference. As shown in Fig. 3, in living medusae these differences are quite obvious (although Figs 3A-C and 3D-E compare *T. rubra* and *T. nutricula*, but the former species from New Zealand closely resembles *T. polycirra*). Fixation and contraction, though, may largely obliterate the morphological differences. The observed differences of the three compared species are summarized in table 1.

Hartlaub (1911) and Russell (1953) regarded *Turris neglecta* Lesson, 1843 as a questionable synonym of *T. polycirra* or *T. nutricula*. According to Lesson (1843), *Turris neglecta* has a size of about 12-15 mm and only 16 tentacles. This is incompatible with *Turritopsis polycirra* and the identity of *Turris neglecta* remains unresolved. The *Turris neglecta* described by Gosse (1853), Wright (1959), and Hincks (1868), however, are without doubt referable to *Turritopsis polycirra*.

TABLE 1: Differences of the *Turritopsis* species discussed in this publication.

character	<i>T. nutricula</i> (eastern Atlantic)	<i>T. polycirra</i> (North Sea)	<i>T. rubra</i> (New Zealand)	<i>T. dohrnii</i> (Mediterranean)
embryo brooded	no	yes	yes	no
reproduction	gonochoristic	hermaphroditic	gonochoristic	gonochoristic
outer portion of radial canals	does not appear to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells	appears to overtop mass of vacuolated cells
mass of vacuolated cells	split into four blocks	four blocks fused into one mass	four blocks fused into one mass	split into four blocks
colour of stomach	yellow to orange	red-orange to red	red-orange to red	?brownish
bell size	3-4 mm, max. 6 mm	4-5 mm	3-7 mm	1.8-2.7 mm
umbrella top	rather flat	rounded	rounded to conical	conical
swelling of tentacle tips	distinctly swollen	not swollen	sometimes slightly swollen	swollen
tentacle number	40-100	up to 90	up to 120	14-32
manubrial pads in young medusae	not reported	unknown	present	present
hydroid colony	branched, mono- or polysiphonic	? stolonal or sparingly branched	branched, mono- or polysiphonic	branched, mono- or polysiphonic

REMARKS ON POLYP STAGE – Although *Turritopsis polycirra* medusae can be quite common in the English Channel (Russell, 1953, as *T. nutricula*), the hydroid stage has only rarely been reported. Actually, the only records appear to be by Billard (1912) and Teissier (1965), who found it at Roscoff. Teissier recorded it on pebbles in the intertidal zone and on old shells in subtidal regions. Billard (1912, as *T. neglecta*) found the hydroid in aquaria. He did not mention gonophores. In addition, it is very likely that *Tubiclava fruticosa* Allman, 1872 is the polyp phase of *T. polycirra*. Especially worth mentioning is its reddish colour, a characteristic trait of several *Turritopsis* hydroids. However, Allman's hydroid from Wales did not bear medusae buds and remains of uncertain identity.

The hydroid has been reared several times from planulae released by the medusa (e. g. Gosse, 1853 as *Turris neglecta*; Wright, 1859 as *Clavula Gossi*; Russell, 1953 as *T. nutricula*). Cultivated hydroids and colonies from nature collected by Prof. J. Bouillon near Roscoff (Brittany) were deposited in the IRSNB and were examined for this study. However, the state of conservation did not permit extraction of information beyond that indicated above under "characteristics". Nevertheless, *Turritopsis polycirra* appears to form only small, sparingly branched colonies. It seems quite unlikely that *T. polycirra* forms large colonies as seen e. g. in *T. dohrnii* or *T. rubra*. Such conspicuous colonies would certainly have been discovered along the coasts of Europe, one of the regions of the world that has been searched for hydroids very intensively.

CONCLUSIONS – Although quite similar in morphology, *Turritopsis* medusae from the western and north-eastern Atlantic differ in reproductive strategy. While the American medusae spawn their eggs into the free water (oviparity), their European counterparts brood fertilized eggs and release fully formed planula larvae (larviparity). There is also a significant difference in the gonad structure: the European medusae are simultaneous hermaphrodites, while American medusae are dioecious. Whether there exist also purely male medusae in the European Atlantic cannot be said at present, because not enough specimens could be examined. None of the prominent authors (e. g. Hartlaub, 1911; Russell, 1953) mentions male medusae, but Keferstein (1862) noted that he had observed male and female medusae. It is also not known whether auto-fertilization is possible. Hermaphroditic hydromedusae are not common, but the phenomenon is known to occur e. g. in *Eleutheria dichotoma* (see Müller, 1908).

The brooding behaviour and the hermaphroditism make the *Turritopsis* medusae of the north-eastern Atlantic quite distinct from *T. nutricula* found in the western Atlantic. Although Russell (1953) attributed only varietal character to this difference, it seems unlikely that animals with such different reproductive strategies form a single biological species. Because there are also other, unrelated differences (table 1), it is justified to regard *T. polycirra* as a valid species and distinct from *T. nutricula*.

The medusa of *Turritopsis polycirra* is very similar to *T. rubra* from New Zealand inasmuch both species brood their embryos, share the same intense red colour, the tightly fused blocks of vacuolated cells, and the high insertion point of the radial canals (Fig. 3A-B). *Turritopsis rubra* differs, however, in being gonochoristic and presumably also in forming large, polysiphonic hydroid colonies (see also table 1).

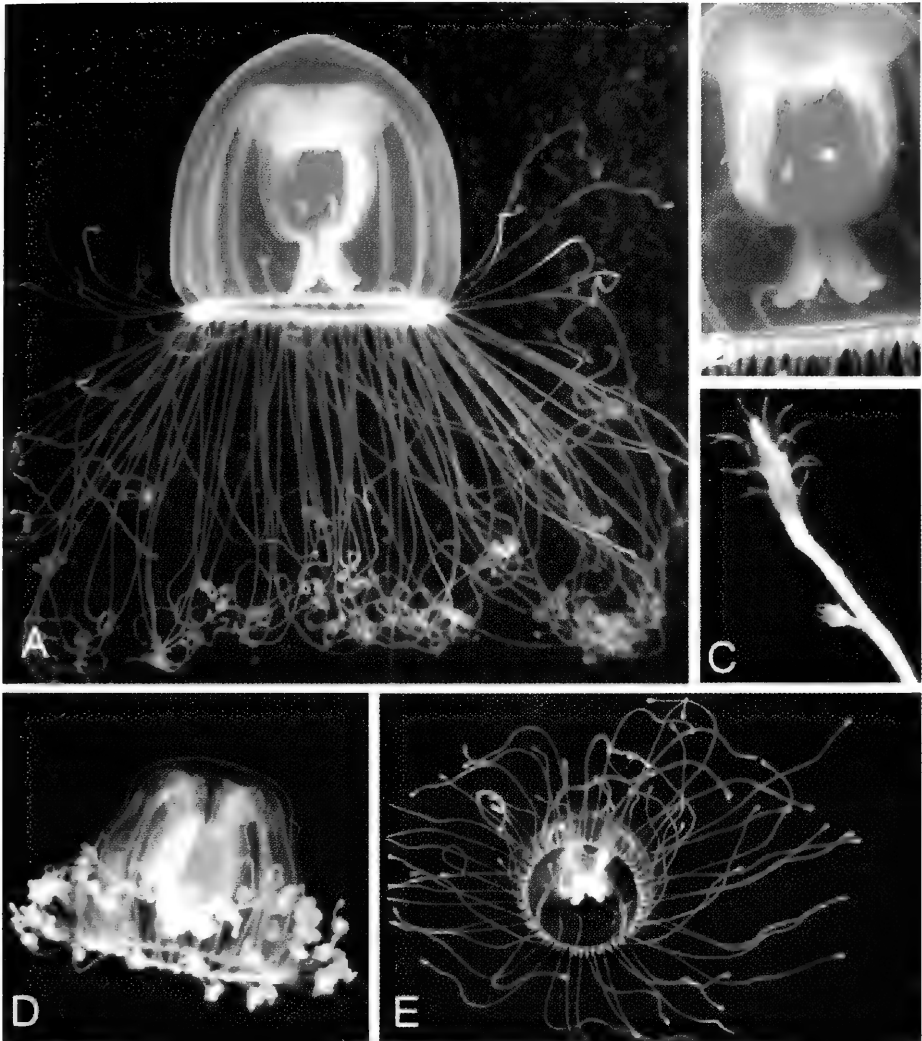


FIG. 3

A-C, *Turritopsis rubra* from New Zealand; this species has almost the same morphology and colour as the European *T. polycirra*. D-E, *Turritopsis nutricula* from Brazil (photographs D-E kindly provided by Dr A. Migotto, São Paulo). A) Brooding female medusa, bell height 4 mm. B) Higher magnification of manubrium with planula larvae. C) Hydroid stage, tentacles somewhat contracted, height of hydranth body about 1 mm. D-E) Medusa, bell size approx. 3 mm, note the difference to *T. rubra* in bell shape, manubrium colour, shape of the vacuolated masses, the swollen tentacle tips, and the entry point of the radial canals.

Another European *Turritopsis* species is the Mediterranean *T. dohrnii*, the status of which is discussed below.

Further potentially valid nominal species within the genus *Turritopsis* are: *Turritopsis fascicularis* Fraser, 1943; *Turritopsis pleurostoma* (Péron & Lesueur,

1810); *Turritopsis chevalense* (Thornely, 1904); *Turritopsis lata* von Lendenfeld, 1885; *Turritopsis pacifica* Maas, 1909; and *Turritopsis minor* (Nutting, 1905). Their reproductive strategies and life-cycles must all be re-evaluated.

***Turritopsis dohrnii* (Weismann, 1883)**

Fig. 4

Dendroclava dohrnii Weismann, 1883: 26; Zoja, 1892: 409; Neppi, 1917: 42, pl. 4 fig. 14.

Tubiclava fruticosa – Riedl, 1959: 611.

[not *Tubiclava fruticosa* Allman, 1872 = ? *Turritopsis polycirra*].

Turritopsis nutricula – Neppi & Stiasny, 1913: 25; Ramil & Vervoort, 1992: 17; Piraino *et al.*, 1996: 304, figs 4-5; Carla *et al.* 2003: 213, figs 1-3.

[not *Turritopsis nutricula* McCrady, 1857].

MATERIAL EXAMINED – Several living polyp colonies collected at Mallorca, depth 2-4 m, July-August 1999 and 2000, initial stages of medusa phase cultivated; some material deposited as MHNG INVE 27123 – Living material from Ischia, Italy, collected July 1993, medusae cultivated for 7 days – Natural History Museum of Vienna, as *Tubiclava fruticosa*, coll. Riedl, Tyrrhenia Expedition, 31.7.1956, on sponge, medusae buds present although tissue somewhat deteriorated (material mentioned in Riedl, 1959).

TYPE MATERIAL – There presumably exists no type material of *T. dohrnii*.

DIAGNOSIS – Hydroid colony of variable height, either sparingly branched with shoots only a few mm high to much branched and polysiphonic colonies up to 35 mm high. Hydranths with 12-20 tentacles. Periderm two-layered (see Schuchert, 1996: fig. 5d). Hydranths in life colourless or pinkish. Newly released medusa with 8-12 tentacles, manubrium with yellow-fluorescent interradial pads (paler to colourless in cultivated animals), vacuolated cells visible. Adult medusa (after Neppi & Stiasny, 1913; Piraino *et al.*, 1996) up to 2.7 mm in height, diameter 3.2 mm, mature specimens with 14-32 tentacles, manubrium reaching to bell margin, tentacles sometimes with terminal swellings, ocelli rust-coloured, gonads brownish, with 4 interradial rust-coloured dots, proximal ends of radial canals swollen through vacuolated gastrodermal cells, the four swellings not fused into a single mass. Sexes separate and females oviparous (Dr. S. Pirano, pers. comm.). Medusa can metamorphose back into polyp stage (Piraino *et al.*, 1996; Carla *et al.*, 2003).

DISTRIBUTION – Western Mediterranean, Adriatic Sea. Type locality: Naples, Mediterranean.

REMARKS – Weismann (1883) used the name *Dendroclava dohrnii* for this species. The spelling of the specific epithet ending with *-ii* is correct and must be maintained (ICZN, 1999: § 31.1.1 and § 31.1.3. The name is meant as a dedication to Anton Dohrn, latinized as *Dohrnii*, which gives in genitive case *dohrnii*).

The initial description of *Turritopsis dohrnii* was based on the hydroid phase only. It was synonymized with *T. nutricula* by Neppi (1917) and her opinion was adopted by nearly all subsequent authors. The only life-cycle studies resulting in mature medusae are described by Piraino *et al.* (1996, as *T. nutricula*) and Carla *et al.* (2003, as *T. nutricula*).

I consider *T. dohrnii* to be a distinct species differing from the European *T. polycirra* and the American *T. nutricula*. *Turritopsis dohrnii* is oviparous and dioecious and thus clearly distinct from the hermaphroditic and larviparous *T. polycirra*. Other differences from the latter species are more gradual: colony size (large polysiphonic

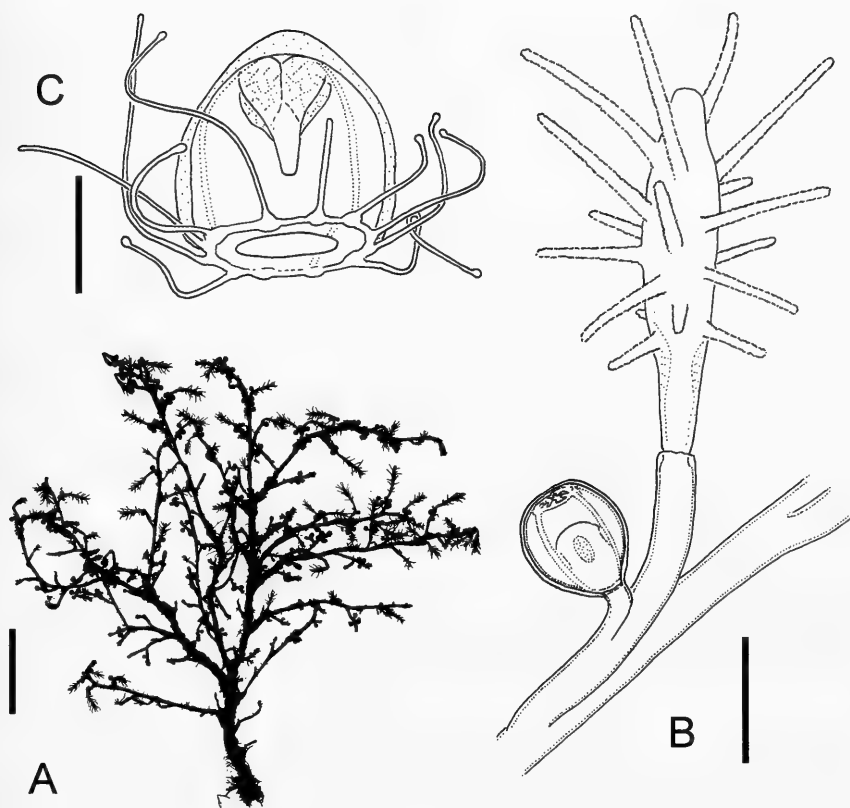


FIG. 4

Turritopsis dohrnii (Weismann, 1883). A) Silhouette of colony, preserved material from Mallorca, scale equals 5 mm. B) Hydranth and medusa bud, tentacles somewhat contracted, after living material from Ischia, scale bar 0.4 mm. C) Young medusae, drawn after photograph in Piraino *et al.* (1996), scale bar 1 mm.

versus small monosiphonic), number of tentacles of the medusa (16-32 versus up to 90), the colour of the gonads (brown versus red), and possibly also the brown spots on the gonads in *T. dohrnii* (the latter detail needs a re-evaluation).

The differences of *T. dohrnii* and the American *T. nutricula* are significant, although they are mostly only gradual. The medusae differ in tentacle numbers, bell size, and the size of the vacuolated masses. The newly released medusae have conspicuous manubrial pads, which have never been reported for *T. nutricula* (comp. Brooks 1886; Brooks & Rittenhouse, 1907; Migotto, 1996). The polyp stage seems to be indistinguishable, although *T. dohrnii* may form larger colonies. According to Migotto (1996), *T. nutricula* forms either monosiphonic or polysiphonic colonies, as in *T. dohrnii*. It seems prudent to regard *T. dohrnii* as separate from *T. nutricula* until more detailed life-cycle studies prove otherwise. Preliminary molecular investigations confirmed that the two belong to two separate lineages (M. P. Miglietta, Duke University, pers. comm.).

While the hydroid phase is relatively common on rocky substrates of the western Mediterranean, *Turritopsis* medusae are much less known. *Turritopsis* medusae have been reported from the Mediterranean by: Hartlaub (1911, Sète, as *T. polycirra*), Neppi & Stiasny (1913, Trieste, as *T. nutricula*), Schmidt (1973, as *T. nutricula*), Dowidar (1984, Egypt, as *T. nutricula*), Goy *et al.* (1991, Lebanon, as *T. nutricula*).

Another record of a Mediterranean *Turritopsis* medusa is *T. pacifica* by Browne (1927). Browne's medusa from Port Said at the Suez Canal was 3.5 mm in size and had 120 tentacles, a number which is significantly higher than observed by Neppi & Stiasny (1913) or Piraino *et al.* (1996). I believe that this medusa was probably not *T. dohrnii* and that it was perhaps an invader from the Red Sea or Indian Ocean. Kramp (1959: 246) likewise stated that *T. nutricula* might have invaded the eastern Mediterranean via the Suez Canal, but is unclear to what morphotype he was referring to or on which evidence he based his assumption.

The records of *T. nutricula* by Schmidt (1973), Dowidar (1984), and Goy *et al.* (1991) from the eastern Mediterranean do not provide sufficient data to evaluate the taxonomic status of their animals.

***Oceania* Péron & Lesueur, 1810**

TYPE SPECIES – Mayer (1910) designated *Oceania armata* Kölliker, 1853 as type species, a species not originally included in the genus *Oceania* by Péron & Lesueur (1810). Mayer's designation is thus currently not valid.

DIAGNOSIS – Anthoathecate medusae with eight or more marginal tentacles not grouped in clusters. Manubrium upon a simple, solid, gelatinous peduncle not formed by vacuolated cells. Manubrium ovoid, diameter at base smaller than in middle, mouth rim studded with a row of spherical nematocyst clusters, each cluster on a short stalk. Ocelli adaxial, on tentacle base. Polyp phase forming stolonal colonies, hydranths with scattered filiform tentacles.

REMARKS – *Oceania* Péron & Lesueur, 1810 originally included species of medusae now referred to several different families and orders (Goy, 1995). First attempts to restrict the scope of the genus *Oceania* were made by Lesson (1843), who used it more in the sense of *Clytia* of present-day authors, thus falling within the order Leptothecata. Forbes (1848), on the contrary, used *Oceania* so that its species would today either fall within the Pandeidae or the Oceanidae as delimited in this publication. Forbes's usage was adopted by Kölliker (1853) when he described *Oceania armata*, and by Gegenbaur (1856) in his taxonomic system of the medusae. Agassiz (1862) returned to the usage of Lesson (1843) and with some ambiguity he even designated a type species. He noted for a conglomerate of species nowadays allocated to several families (Agassiz, 1862: 346, footnote 2): "I see, however, no reason why the name Nucleiferae, which he [Lesson] proposed for the old Forskalian type, should not be retained for this family, and the name *Oceania* and *Oceanidae* applied specifically, as Lesson has done, to *Oceania phosphorica*, which Péron & LeSueur place in the first section of the genus. This corresponds to the genus *Thaumatias* of modern writers." The sentence is somewhat ambiguous and it is debatable whether this must be seen as

a valid type-species designation (comp. ICZN § 67.5.3), but in the following taxonomic overview, Agassiz (1862) used the genus *Oceania* approximately in the sense of the present-day usage of *Clytia*. *Oceania phosphorica* Péron & Lesueur, 1810, the species which Agassiz considered typical for the genus, is likely a synonym of *Clytia hemisphaerica* (see Goy, 1995). Following authors adopted either Forbes's or Lesson's view of the genus. This caused so much confusion that Haeckel (1879) abandoned the genus *Oceania*. In order to settle the dispute, and in order to stabilize the prevailing usage, Mayer (1910: 147) designated *Oceania armata* Kölliker, 1853 as type species for the genus *Oceania*. This settled the dispute and all following authors, notably also Kramp (1959, 1961, 1968) in his influential synopses, used *Oceania* as proposed by Mayer (1910). However, Mayer's type species designation is not in accordance with provisions of the ICZN currently in use (Calder, 1988b). The designation is invalid because *O. armata* was not one of the originally included species (ICZN § 69.1). This contrasts with the usage of the genus *Oceania* which was employed almost exclusively for the species *Oceania armata*, a circumglobal species that is well known and has regularly been reported in the literature of the last 150 years. Nomenclatural stability is thus severely threatened if the genus *Oceania* were to be replaced by a new name, or even worse, if recognized as a senior synonym of the leptomedusan genus *Clytia* Lamouroux, 1812. Therefore, after the publication of this study, a case will be made to conserve *Oceania* in its current meaning by asking the International Commission on Zoological Nomenclature to rule that *Oceania armata* is the type species of the genus, notwithstanding the fact that it was not an originally included species and overruling the potential type-designation of Agassiz.

If the genus *Oceania* Péron & Lesueur, 1810 is accepted as valid, then automatically also the family group name Oceanidae Eschscholtz, 1829 becomes available.

Turritopsis and *Oceania* medusae resemble each other quite closely, but they can be distinguished (see remarks under genus *Turritopsis*).

Oceania armata Kölliker, 1853

Fig. 5

Oceania armata Kölliker, in Gegenbaur *et al.*, 1853: 323; Metschnikoff, 1886: 78, pl. 1 figs 32-39; Mayer, 1910: 147, figs 80-81; Uchida 1927: 219; Kramp, 1959: 99, fig. 63; Kramp, 1961: 65; Kramp, 1968: 27, fig. 67; Brinckmann-Voss, 1970: pl. 4 fig. 2; Bouillon, 1980: 308; Bleeker & Van der Spoel, 1988: 230, fig. 6; Bouillon, 1995: 224; Schuchert, 1996: 15, fig. 4a-c.

Oceania flavidula – Gegenbaur, 1856: 223, pl. 7: fig. 4.

[not *Oceania flavidula* Péron & Lesueur, 1810 (= *Laodice undulata* (Forbes & Godsir, 1851))].

Turritopsis armata – Haeckel, 1879: 65.

Callitiara polyophthalma Haeckel, 1879: 67, pl. 3 figs 1-5.

Conis cyclophthalma Haeckel, 1879: 55, pl. 4 fig. 1; Hartlaub, 1913: 342, synonym; Kramp, 1955: 152, synonym.

Tiarella parthenopia Trinci, 1906: 208, figs.

MATERIAL EXAMINED – MHNG INVE 32787, Naples, coll. 1892 – MHNG INVE 34177, Naples, det. Hartlaub, 1 medusa – MHNG INVE 31178, Villefrance-sur-Mer, France, det. Hartlaub, 5 medusae.

TYPE MATERIAL – There presumably exists no type material of *O. armata*.

DESCRIPTION – Mature medusa 5-10 mm high, maximal bell diameter about the same as height, umbrella bell-shaped with flat top, jelly uniformly thin. Manubrium on

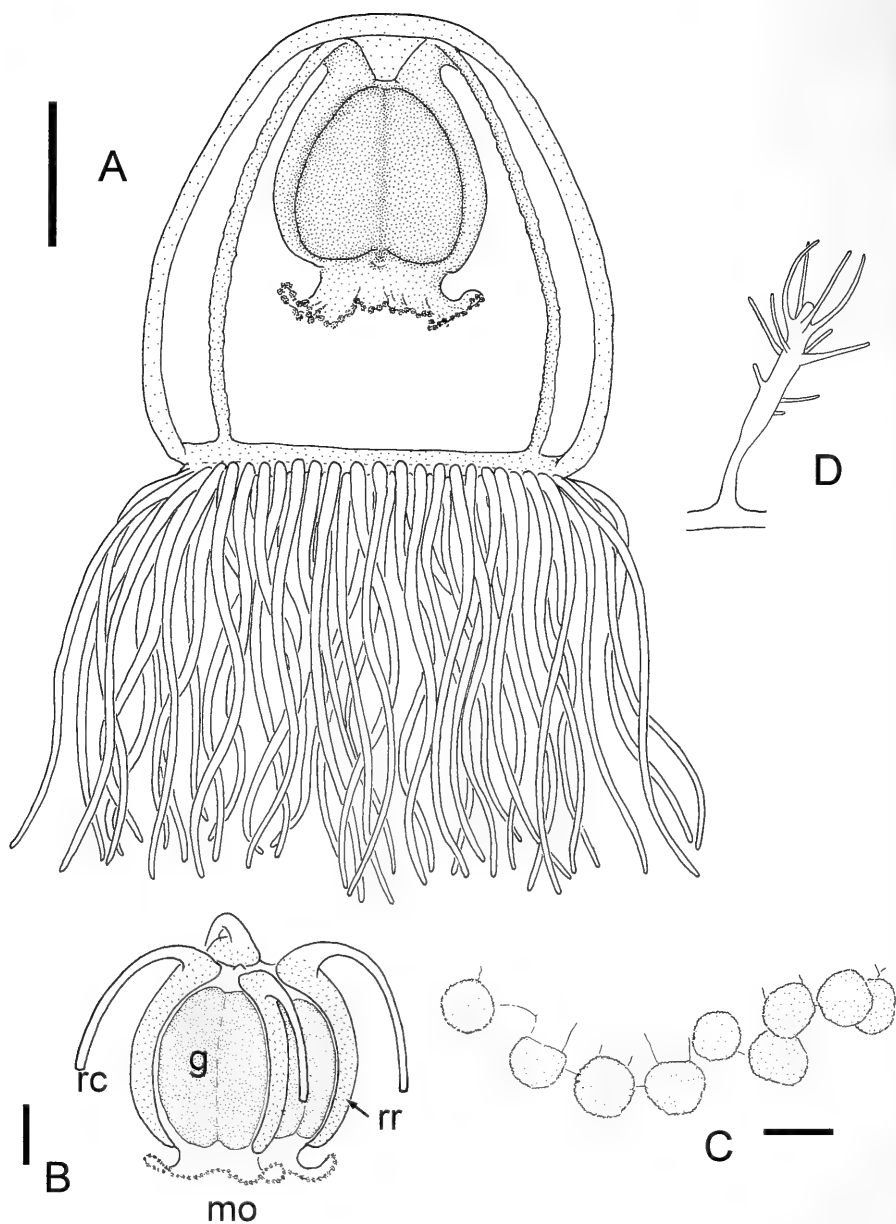


FIG. 5

Oceania armata K  lliker, 1853, A-C, after preserved material from Naples; D, modified after Metschnikoff (1886). A) Mature medusa, scale equals 2 mm. B) Manubrium with parts of radial canals, scale equals 1 mm, g = gonad, mo = mouth, rc = radial canal, rr = radial rib. C) Higher magnification of mouth rim fringed with pedicellate nematocyst clusters, scale 0.1 mm. D) Young hydranth, no scale available.

a transparent, shallow peduncle without vacuolated cells. Manubrium large, up to 2/3 of subumbrellar height, ovoid, manubrium base constricted, with funnel-shaped mouth region. Stomach and mouth region distinctly cruciform in cross-section. Radial canals where joining manubrium funnel-like dilated and composed of large cells, continued on manubrium as radial ribs like four clasping claws (Fig. 5B). Mouth rim crenulated, with four prominent perradial lips. Margin of mouth with a continuous row of spherical nematocyst clusters, these usually on short pedicels. Gonads smooth, on interradial surface of stomach. Four quite broad radial canals, margins occasionally jagged, circular canal broad. Marginal tentacles tapering, 80-120 in number, longer than bell (preserved sample), gastrodermis chordoid. Origins of tentacles somewhat alternately displaced adaxially and abaxially. Each tentacle with a slight proximal swelling beginning shortly after origin. Adaxial ocellus near tentacle base. Nematocysts: microbasic euryteles, desmonemes. Colours (after Haeckel, 1879): Manubrium and gonads yellow or brown-yellow, mouth-lips orange or red, radial canals, ring canal and tentacles yellow, ocelli brown-red. Egg size about 0.27 mm. Polyp stage (after Metschnikoff, 1886) colonial, with creeping, ramified stolons. Hydranths on short, periderm-covered pedicel. Hydranth spindle-shaped with conical hypostome. With around 13 filiform tentacles in up to four whorls.

BIOLOGY – Usually occurring in depths of less than 200 m, but not at surface (Kramp, 1965).

DISTRIBUTION – Mediterranean, coasts of Senegal and Gambia, Canary Islands, Cape Verde, Azores, Portugal, Spain; West Indies; Japan, New Zealand, Tasman Sea. The northern limit in Europe seems to be Portugal. Type locality: Mediterranean.

REMARKS – The polyp *Oceania armata* is known only from the rearing experiments of Metschnikoff (1886) and has never been found in nature. The origin of medusae buds is also not known.

Bleeker & van der Spoel (1988) described the morphologically similar *Oceania tydemani* based on a single medusa taken south-west of the Azores. *Oceania tydemani* differs from *O. armata* in having more tentacles (180) and the nematocyst clusters of mouth margin are absent over four short interradial stretches.

The identity of *Oceania flavidula* Péron & Lesueur, 1810 is pertinent to the question of the validity of the genus *Oceania* (see remarks under genus *Oceania*). Gegenbaur (1856) believed *O. flavidula* and *O. armata* to be conspecific. The plates of Péron & Lesueur published by Goy (1995) now allow to identify *O. flavidula* as a synonym of *Laodice undulata* (Forbes & Godsir, 1851). Thus, the genus *Oceania* sensu Péron & Lesueur, 1810 did not originally include *Oceania armata* Köl liker, 1853.

***Corydendrium* van Beneden, 1844 (emended)**

SYNONYM – *Soleniopsis* Ritchie, 1907.

TYPE SPECIES – *Sertularia parasitica* Linnaeus, 1767.

DIAGNOSIS – Erect, branching or stolonial hydroid colonies, monosiphonic or polysiphonic. In branching colonies, branches and hydranth pedicels adnate to other branches over part or almost all their length. Perisarc firm, terminating near hydranth base, tubes of sister-branches nested. Hydranths spindle- to club-shaped; filiform

tentacles scattered over much of hydranth body. Gonads formed within perisarc tubes of branchlets or at the end of branchlets and thus replacing a hydranth. Gonads gastrodermal.

REMARKS – The taxonomic history of this genus was reviewed by Calder (1988a). Kramp (1935) has not been followed in merging *Corydendrium* with *Turritopsis* (see discussion above). As mentioned in the introduction to the family, the genus *Corydendrium* is here restricted to Oceanidae which have at least one of the following synapomorphies: (I) gonads within the perisarc tubes of hydranth pedicels or branchlets, (II) nested perisarc tubes.

Clearly also a member of the genus *Corydendrium* in the sense of the author is the Japanese *C. brevicaulis* Hirohito, 1988. This species is quite important in discussions of the scope of the genus as it forms either stolonial or branched colonies. In its morphology, this species otherwise resembles *C. parasiticum* so closely that it could arguably seen only as a variant of it. The generic diagnosis was therefore modified to include stolonial colonies to permit the inclusion of *C. brevicaulis* Hirohito, 1988.

Hirohito (1988) also described another *Corydendrium*, namely *C. album*. It resembles closely *Turritopsoides brehmeri* Calder, 1988b and should be transferred to the genus *Turritopsoides* if the so far unknown female gonophores of *C. album* will prove to be identical.

Fiorini (1977) argued that the reproductive organs of *C. parasiticum* are probably not homologous to a gonophore and thus to a vestigial medusa. They are most likely a composite structure derived from a polyp with several gonophores (the term gonophore must be restricted to gonad-bearing structures that can be homologized with a single medusa bud). Such a composite gonad-bearing organ is thus better referred to as a gonangium (see also discussion in Thiel, 1962). Contrary to most other hydrozoans, the germ cells of *Corydendrium parasiticum* and of the males of *C. dispar* remain in the gastrodermis (Weismann, 1883; Fiorini, 1977; Kramp, 1935). Other species referred here to *Corydendrium* should be examined if they have similar gonangia, which would consolidate it as an additional synapomorphy for the genus. Germ cells located in the epidermis represent a synapomorphy for the Hydrozoa (Schuchert, 1993). The gastrodermal gonads of some *Corydendrium* species must be seen a character reversal. All other related taxa have epidermal gonads.

Corydendrium corrugatum Nutting, 1905 from Hawaii likely also belongs to the genus *Corydendrium*, although its reproductive structures remain unknown (see Schuchert, 2003b). The same holds true for *C. flabellatum* Fraser, 1938 from the tropical eastern Pacific and *C. fruticosum* Fraser, 1914 from Vancouver Island (north-eastern Pacific). *Corydendrium splendidum* Boone, 1938 is a synonym of *Pennaria disticha* Goldfuss, 1820 (see Cooke, 1977).

The European fauna includes only two species, namely *Corydendrium parasiticum* (Linnaeus, 1767) and *Corydendrium dispar* Kramp, 1935.

Corydendrium parasiticum (Linnaeus, 1767)

Fig. 6

Sertularia parasitica Linnaeus, 1767: 1315.

? *Solenopsis dendriiformis* Ritchie, 1907: 495, figs 142-143, pl. 26 fig. 1.

? *Corydendrium sessile* Ritchie, 1910a: 802, pl. 76 figs 1-2.

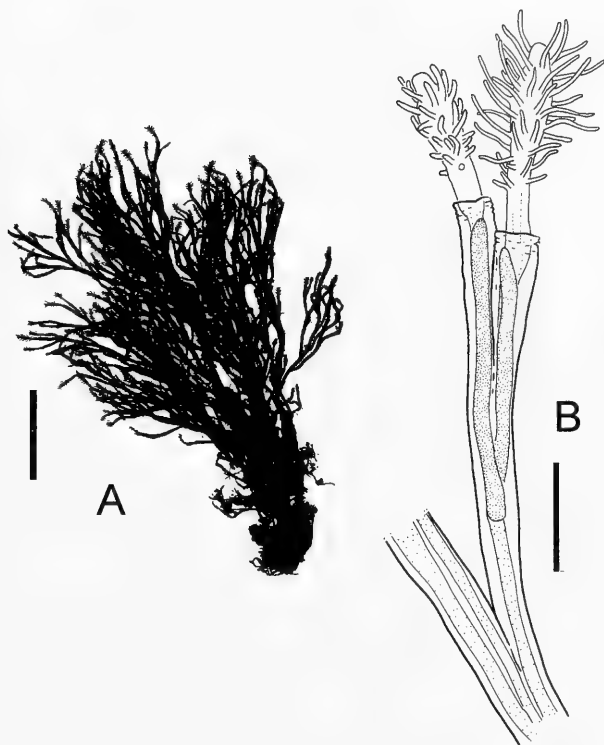


FIG. 6

Corydendrium parasiticum (Linnaeus, 1767), after preserved material from Naples. A) Colony silhouette, scale equals 1 cm. B) Distal branches with two hydranths, note gonads (stippled) in perisarc tube of pedicels and adnate branches, scale equals 1 mm.

not *Clava* (*Corydendrium*) *parasiticum* – Bonnevie, 1899: 39 [= *Corydendrium dispar* Kramp, 1935].

Corydendrium parasiticum – Weismann, 1883: 34, fig. 7, pl. 14 figs 1-9, pl. 15 figs 1-5, pl. 16 figs 1-2, 4; Neppi, 1917: 43, figs 7-8; Rossi, 1971: 20, fig. 6L; Millard, 1975: 72, fig. 24B-D; Wedler & Larson, 1986: 82, fig. 5C; Rees & Vervoort, 1987: 12, bibliography; Calder, 1988a: 6, figs 3-4; Hirohito, 1988: 66, fig. 21 a-c, pl. 2 fig. B; Migotto, 1996: 11, fig. 2e; Watson, 1999: 2, fig. 2A-E; Calder *et al.* 2003: 1176, fig. 2.

MATERIAL EXAMINED – MHNG INVE 25127, Naples, Italy, fertile males, very profuse colony – MHNG INVE 31489, Naples, Italy, coll. 1892 – MHNG INVE 31490, Naples, Italy, coll. 1896.

TYPE MATERIAL – No type material was localized.

DESCRIPTION – Colonies bushy, much branched, polysiphonic, 2-5 cm in height (reportedly up to 16 cm). Perisarc stiff, smooth or encrusted with silt, not annulated, terminating below hydranths, sometimes terminal part slightly dilated and wrinkled. Branches adnate for some distance, then diverging at acute angle. Perisarc tubes of side-branches nested at their origins. Diameter of branches 0.4-0.5 mm, terminal tubes 0.3 mm. Hydranths elongated, cylindrical to fusiform, 1-3 mm long, diameter up to 0.35 mm, with 20-40 filiform tentacles scattered over most of hydranth body.

Hypostome prominent, dome-shaped. Sexual organs tubular structures, length 3 mm and more, arising as side branches of hydranth pedicels, initially wholly contained within perisarc tube, mature eggs extruded from perisarc but remaining attached near end of tube until developed into planulae, thus larviparous (Neppi, 1917; Wedler & Larson, 1986). Structure of sexual organs simple, bi-layered, gametes in gastrodermis. Nematocysts: microbasic euryteles and desmonemes.

BIOLOGY – Grows most often on rock. The fertile period in the Mediterranean is from August to September, while colonies are present from June to October (Lo Bianco, 1909). Motz-Kossowska (1905) obtained fertile colonies from the Balearic Archipelago in August. Neppi (1921) found colonies during June and August, and they were also fertile during this period. In the Mediterranean, the species seems to be only locally abundant, with most records coming from Naples. Intensive searches for it at localities near Banyuls-sur-Mer (Motz-Kossowska, 1905), Island of Medes (Gili, 1982) and near Genoa (Boero & Fresi, 1986) were unseccussful.

OTHER INFORMATION – The microscopic structure was investigated in detail by Weismann (1883) and Fiorini (1977). The ultrastructure of the planula and the oocytes were investigated by Glätzer (1970, 1971). The early development was examined by Neppi (1917) and Glätzer (1971).

DISTRIBUTION – Perhaps circumglobal in tropical and subtropical seas: along the European coasts confined to the Mediterranean (Weismann, 1883; Neppi, 1917), also coasts of western and southern Africa (Ritchie, 1907; Millard, 1975), tropical western Atlantic (Wedler & Larson, 1986; Calder, 1988a; Migotto, 1996), Indian Ocean (Millard & Bouillon, 1973; Rees & Vervoort, 1987), Indonesia (Vervoort, 1941; Schuchert, 2003b), coasts of northern Australia (Watson, 1999), tropical western Pacific (Leloup, 1937, as *C. dendriforme*), north-western Pacific (Hirohito, 1988), ? tropical eastern Pacific (Fraser, 1938, as *C. flabellatum*). Depth range about 1-90 m.

REMARKS – The taxonomic history and synonymy of this species are given by Calder (1988a) and need not be repeated here in detail. Vervoort (1941), Millard (1975), and Calder (1988a) considered *Corydendrium dendriforme* (Ritchie, 1907) from the Cape Verde Islands conspecific with *C. parasiticum*. This contrasts with Rees & Thursfield (1965) who re-examined the type material of *C. dendriforme* and kept it distinct. Both species reportedly differ in the more arborescent colony of *C. dendriforme* versus the more bushy one of *C. parasiticum* (see fig. 6). Although the arguments in favour of a conspecificity appear more convincing, a definite answer is not possible at the moment. A detailed comparison of the populations from the Cape Verde Archipelago with those from adjacent regions is needed to provide the necessary arguments. *Corydendrium dendriforme* (and also *C. sessile*) are thus treated as questionable synonyms of *C. parasiticum*. The material from the Strait of Gibraltar reported by Ramil & Vervoort (1992) as *C. parasiticum* is somewhat atypical and perhaps does not belong to this species.

Corydendrium dispar Kramp, 1935

Fig. 7

Clava (*Corydendrium*) *parasiticum* – Bonnevie, 1899: 39.
[not *Corydendrium parasiticum* (Linnaeus, 1767)].

Corydendrium dispar Kramp, 1935: 1, figs 1-4.

not *Corydendrium dispar* – Rasmussen, 1973: 22 [= *Pachycordyle navis* (Millard, 1959)].

TYPE MATERIAL EXAMINED – ZMUC, holotype, Kungsbackafjord, Sweden, coll. 26 Jun 1928, 26 m – ZMUC, paratype, Kvittingsøy, Norway.

OTHER MATERIAL EXAMINED – BIOFAR collection (Nørrevang *et al.*, 1994), kept by Kaldbak Marine laboratory, The Faroes: Station 8 (62.29°N 5.40°E, 171 m, 17 Jul 1987, on bivalve shell); station 165 (62.18°N 4.97°E, 184 m, 07 May 1988), slides of this material deposited as MHNG INVE 33555; station 204 (62.16°N 5.88°E, 158 m, 11 May 1988, on *Abietinaria fusca*).

DESCRIPTION – (after Kramp, 1935 and examined material) Colonies forming delicate, erect shoots, less profuse than *C. parasiticum*, 0.5 - 2 cm in height, reportedly up to 6.5 cm. Stolons creeping, ramified, anastomosing. Shoots irregularly branched, entirely monosiphonic or polysiphonic in lower parts of the shoots, branches adnate to each other over variable distances, diameter of single branch up to 0.2 mm, perisarc tubes at origin of branches nested, perisarc wrinkled, generally double-layered, inner layer thick and firm, outer layer membranous. Hydranths spindle-shaped, 0.6 mm in preserved material, hypostome dome-shaped, 16-20 filiform tentacles scattered over most of hydranth body. Reproductive organs not within perisarc tubes of branchlets, arising like hydranths at end of side-branches, covered by very thin perisarc membrane. Male sexual organs are sessile sporosacs, oblong-elliptic or -ovoid, length 0.7 mm, diameter 0.4 mm, on short pedicels; structure sac-like, with thin epidermis and thick gastrodermis containing the gametes. Mature female organs insufficiently known, likely sessile sporosacs, spherical, diameter up to 1.2 mm.

BIOLOGY – Known substrates are shells and hydroids (Kramp, 1935; this study). Occurs in fully marine environments only. Depth range: 26 to 184 m.

DISTRIBUTION – Along Swedish and Norwegian coast north to Trondheim Fjord (Kramp, 1935), The Faroes. Type locality: Kungsbackafjord, south of Gothenburg, Sweden, 26 m (Kramp, 1935).

REMARKS – *Corydendrium dispar* Kramp, 1935 is recorded here for the first time in waters of the Faroe Islands. The samples contained only male specimens and the mature female reproductive structures are still imperfectly known. While the male structures are only simple sacs without any recognizable vestiges of a medusa structure, the initial developmental stages of female ones suggest a medusoid origin (Kramp, 1935).

The material recorded by Rasmussen (1973) as *C. dispar* was re-examined and identified as *P. navis*. See remarks under this species.

Merona Norman, 1865

TYPE SPECIES – *Tubiclava cornucopiae* Norman, 1864 by monotypy.

DIAGNOSIS – Stolonal hydroid colonies, polyps polymorphic with gastrozooids, gonozooids and nematophores. Hydranths with scattered filiform tentacles and perisarc-covered caulus. Gonozooids reduced, without mouth or tentacles, thus blastostyle-like, bearing numerous gonophores. Gonophores sessile sporosacs. Defensive zooids small, arising from stolons, in funnel-shaped perisarc tube.

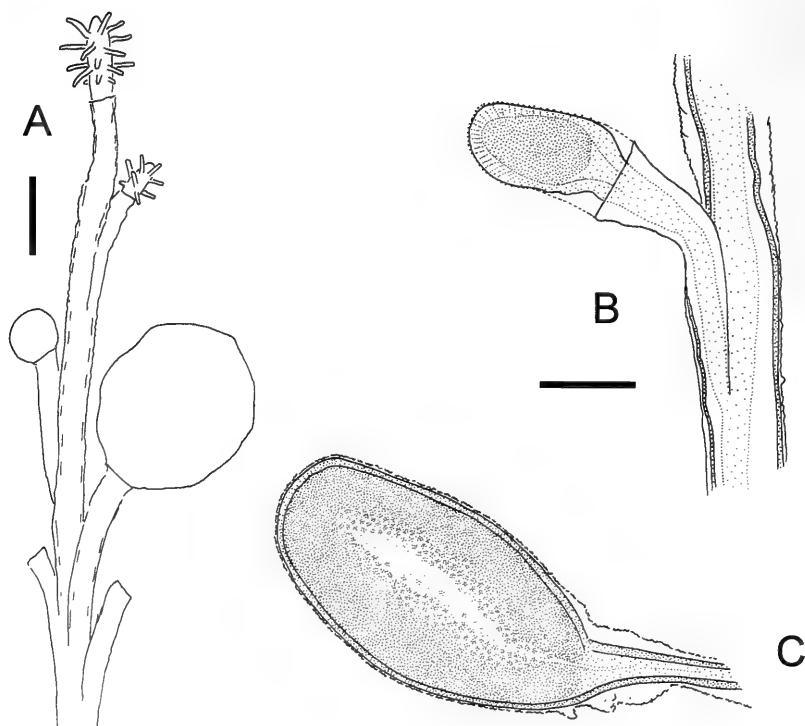


FIG. 7

Corydendrium dispar Kramp, 1935; A, after paratype material; B-C, after preserved material from The Faroes. A) Part of shoot, the putative female sporosacs were empty in this material, scale equals 0.5 mm. B) Branch with young male reproductive structure, optical section, scale bar 0.2 mm. C) Mature male reproductive organ, optical section, same scale as B.

REMARKS – The gonophores of *Merona* arise on blastostyles that can either be interpreted as being derived evolutionary from a hydranth or from a hydranth pedicel. Their simple structure does not lend itself to an easy answer. If the blastostyles are derived from a hydranth body, this would be problematic because in all other Oceanidae the gonophores arise on the pedicels or stolons (see above). The alternative interpretation that the gonozooids are homologous to hydranth pedicels only is much better compatible with the scope of the family as outlined in this publication.

***Merona cornucopiae* (Norman, 1864)**

Fig. 8

Tubiclava cornucopiae Norman, 1864: 82, pl. 9 figs 4-5; Hincks, 1868: 11, pl. 2 fig. 2; Allman, 1872: 258; Fraser, 1937: 23, fig. 4; Fraser, 1944: 36, fig. 4.

Merona cornucopiae – Broch, 1916: 40, pl. 2 fig. 17, fig. L; Rees, 1956: 499, figs 1-3; Cabioch, 1965: 401, figs 1-3; Millard & Bouillon, 1973: 28, fig. 3H-J; Millard, 1975: 74, fig. 25; Medel, García-Gómez & Bouillon, 1993: 515, figs 1-2B; Ramil *et al.*, 1998: 184, fig. 2a-b.

MATERIAL EXAMINED – ZMUC, Denmark, Groves Flak, 25 m, 17 May 1923, on scaphopod, det. Kramp, infertile – ZMUC, Faroe Islands, Skalbünd, 7 Jun 1899, on bivalve shell, much

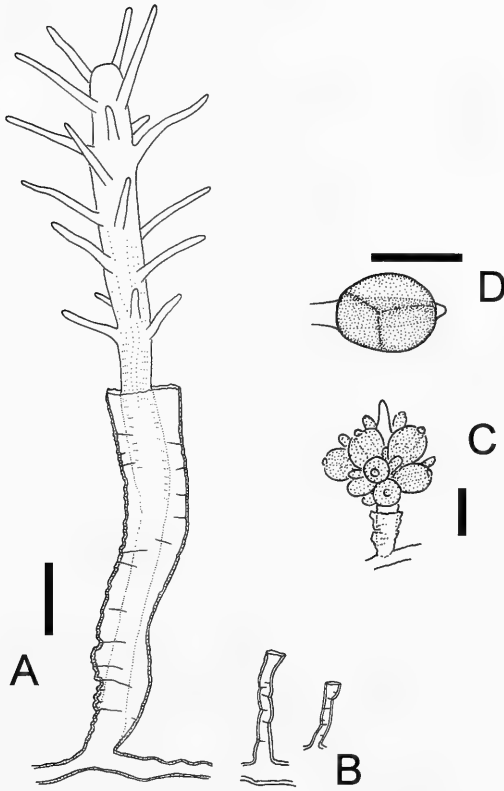


FIG. 8

Merona cornucopiae (Norman, 1864), after preserved material from Roscoff. A) Hydranth, quite expanded, scale equals 0.2 mm. B) Nematothecae on stolons, same scale as A. C) Blastostyle with female gonophores, scale equals 0.2 mm. D) Female gonophore, scale equals 0.1 mm.

damaged, with blastostyles – IRSNB, France, Brittany, Roscoff, numerous colonies on shells of *Turritella* spec. and *Nassarius* spec. inhabited by *Phascolion* spec., not well preserved, one blastostyle seen – BMNH 1956.11.7.1, Brittany, Baie de Morlaix, off. Callot, 22-23 Jun 1955, 15-25 m, on bivalve and *Turritella*, coll. W. J. Rees (material of Rees, 1956), one colony with female gonophores – BMNH 1941.3.20.516, English Channel, Eddystone, 4 Jun 1898, coll. E. T. Browne (material described in Rees, 1956), soft tissues quite damaged, several blastostyles with female gonophores present.

TYPE MATERIAL – The type material of *M. cornucopiae* is kept by the BMNH (Rees, 1956).

DESCRIPTION – (after examined material, and Rees, 1956) Colonies stolonal, never branched, stolons creeping, reticulated or coalesced into mat. Gastrozooids consisting of a perisarc-covered pedicel and a terminal hydranth. Living tissue of hydranth pedicels not well demarcated from hydranth body. Pedicels in wide perisarc tube, the latter 1-5 mm in height, diameter at distal end double or more the basal diameter (0.1-0.14 mm), perisarc thus cone-shaped, often slightly bent or curved, irregularly corrugated, often coated by mud and fine sand grains. Contracted hydranth able to withdraw almost completely into perisarc tube. Relaxed hydranths 1-5 mm,

rod- to slightly spindle shaped, with 16-20 long, filiform, tapering tentacles scattered over distal half or more. Hypostome dome-shaped. High gastrodermal cells in proximal half of hydranth body, apparently vacuolated. Colonies dioecious. Gonophores arise on blastostyles with a short basal perisarc cone as in the hydranths. Gonophores in a dense cluster at distal end of blastostyle. In females, blastostyles with pointed tip that may slightly overtop gonophore cluster, 15-20 gonophores per blastostyle. Gonophore ovoid when mature, length up to 0.2 mm, with distinct stalk, continued through gonophore as spadix, distal part of spadix slightly protruding like nipple, up to six eggs per gonophore. Male blastostyles (after Medel *et al.*, 1993) shorter, gonophores more dense, spherical, spadix perhaps (?) not protruding. Nematophores facultatively present, arising from stolons, about 0.3 mm in height, simple tentacle-like, within thin perisarc tube, the latter at distal end widening funnel-like, tip of nematophore with concentration of large euryteles. Nematocysts (after Cabioch, 1965): large microbasic eurytele (19-22) x (5) μm , discharged shaft about two times as long as capsule; medium sized microbasic eurytele (13-14) x (5) μm , shaft as long as capsule, mainly on tentacles; small microbasic eurytele, (8) x (3) μm , shaft as long as capsule, mainly on tentacles; desmonemes (5) x (3) μm . Colours in life: Hypostome intense white, gastrodermis of hydranth body-orange brown to scarlet, fading in non-tentacular portion into a uniformly pale tint.

BIOLOGY – *Merona cornucopiae* grows predominantly on shells of molluscs such as *Glycimeris*, *Aporrhais*, *Dentalium*, *Turritella* and others, very often on *Turritella* shells inhabited by the sipunculid *Phascolion strombi*. Occurrence is on sediment bottoms in depths of 10-274 m. Fertile specimens were collected at Plymouth in May and June (Rees, 1956), at Roscoff June-July (Teissier, 1965), at Oslofjord end of April (Christiansen, 1972), at Trieste January-February (Graeffe, 1884).

DISTRIBUTION – British Isles (Rees, 1956), Brittany (Rees, 1956; Cabioch, 1965), Faroes (Broch, 1916), Norway (Christiansen, 1972), Spain (Ramil *et al.*, 1998; Medel & López González, 1996), Mediterranean (Graeffe, 1884), north-western Atlantic (Fraser, 1944), north-eastern Pacific (Fraser, 1937), South Africa (Millard, 1975), Seychelles (Millard & Bouillon, 1973). Type locality: Shetland Islands.

REMARKS – Medel *et al.* (1993) described what they considered a sexual dimorphism of the blastostyles of *Merona cornucopiae*. They found that the female blastostyles are longer and they have their gonophores distributed over a larger area, resulting in a less dense arrangement than in males. In the present study, only females were observed and the findings of Medel *et al.* could therefore not be verified. It nevertheless appears that some of the differences are probably only due to different states of contraction and different ages. Rees (1956: figures 1 and 2) shows both types of blastostyles, but both are females (a re-examination of Rees's material confirmed this). The apparent density of the female sporosacs also depends also on how many eggs there are present. A partial spawning results in an apparent reduction of the density of sporosacs, because only the thin spindle-shaped spadices remain of the initially oviform sporosacs.

Merona ibera Medel, Garcia-Gomez & Bouillon, 1993 and *M. cornucopiae* can be distinguished only by their female gonophores. At least for the Mediterranean, it is

therefore not possible to reliably identify *Merona* species without female gonophores. Some of the records of *Merona cornucopiae* from the Mediterranean (e. g. Motz-Kossowska, 1905) are thus perhaps referable to *M. ibera*. Graeffe's (1884, as *Tubiclava cornucopiae*) material from Trieste had four eggs per gonophore. It thus corresponds more with *M. cornucopiae* than with *M. ibera*.

***Merona ibera* Medel, Garcia-Gomez & Bouillon, 1993**

Merona ibera Medel *et al.*, 1993: 513, figs 2C-D & 3A-C.

TYPE MATERIAL – The type material of *M. ibera* is kept by the Museo Nacional de Historia Natural (Madrid) and the RMNH.

DIAGNOSIS – Similar to *Merona cornucopiae*, but female blastostyles smaller and gonophores placed more distally, eggs smaller (37-60 μm), more eggs per gonophore (>12 per gonophore), female gonophore spindle-shaped, distal end of spadix with button of nematocysts.

DISTRIBUTION – Known from type locality only: Algeciras Bay, Strait of Gibraltar, Mediterranean, 21 m, on bivalve *Gouldia minima*.

REMARKS – See under *M. cornucopiae*.

***Rhizogeton* L. Agassiz, 1862**

TYPE SPECIES – *Rhizogeton fusiformis* L. Agassiz, 1862.

DIAGNOSIS – Stolonal hydroid colonies, polyps monomorphic, hydranths either sessile or with a perisarc-covered caulus. Hydranths with scattered filiform tentacles covering at least half of hydranth body. Nematophores absent. Gonophores sessile sporosacs arising from stolons.

REMARKS – Calder (1988a) thought that it might be necessary to split this genus and proposed the new genus *Rhizodendrium*. He held the genus *Rhizodendrium* distinct from *Rhizogeton* on account of the following characters: the hypostome is short and dome-shaped instead of very elongate and conical, it has 20 or more tentacles instead of about 10, its gonophores are more rounded than fusiform. The gonophores of *Rhizodendrium sterreri* Calder, 1988, the type species of the genus *Rhizodendrium*, are so far unknown. The difference in the shape of the gonophores was therefore based on *Rhizogeton nudus* and *R. eozense* Yamada, 1964, which according to Calder (1988a) should be transferred to the genus *Rhizodendrium*. Although the differences in the shape of the gonophore are not so apparent (Dons, 1912), *Rhizogeton fusiformis* appears otherwise to be distinct from *R. nudus* (comp. Fig. 9 and figure 3 in Fraser, 1944). The proposal of Calder (1988a) to separate them into two genera could therefore be justified. If the gonophores of *R. sterreri* are discovered and independent data including DNA sequences show that *Rhizogeton* and *Rhizodendrium* species do not form a monophyletic group, then Calder's proposal should be followed. But because the gonophores of the type species of *Rhizodendrium* are so far unknown, and in order to maintain nomenclatural stability, only the genus *Rhizogeton* is used here.

***Rhizogeton nudus* Broch, 1909**

Fig. 9

Rhizogeton nudum Broch, 1909: 137, fig. 1; Antsulevich & Polteva, 1986: 967, fig. 2; Jones, 1992: 721, fig. 1; Schuchert, 2001a: 20, fig. 10A-C.

Rhizogeton fusiformis – Browne, 1897: 243.

[not *Rhizogeton fusiformis* L. Agassiz, 1862].

Rhizogeton nudus – Dons, 1912: 53, fig. A-C; Calder, 1972: 223, pl. 2 fig. 1.

Rhizodendrium nudum – Calder, 1988a: 11.

MATERIAL EXAMINED – Material from Greenland and Iceland, see Schuchert (2001a).

TYPE MATERIAL – The type material of *R. nudus* could not be located.

DESCRIPTION – Colonies stolonial, stolons creeping, ramified. Hydranths appearing sessile, without distinct pedicel, at base a short beaker of very thin perisarc, usually invisible. Hydranths up to 2.5 mm in height, rod-shaped, with 14–19 tentacles, these scattered in distal half to distal third of hydranth. Tentacles with chordoid gastrodermis, tentacles smooth, tapering, quite long and thin, lengths unequal, proximal ones shorter. Hypostome dome-shaped. High gastrodermal cells in proximal half of hydranth body, apparently vacuolated. Gonophores arising from stolons and developing into sessile sporosacs without canal system or velum but with spadix; with short pedicel enveloped by perisarc, young sporosacs also enveloped by very thin, filmy perisarc. Female sporosacs ovoid to spindle-shaped, diameter 0.35–0.45 mm, length 0.6–0.7 mm, with 3–5 eggs, at maturity the sporosac envelope disappears but eggs and developing embryos stick to the spadix. Male sporosacs oblong ellipsoids, about the same size as female sporosacs. Nematocysts: microbasic euryteles, $7 \times 3 \mu\text{m}$; desmonemes $5 \times 3 \mu\text{m}$. Colour in life: pinkish.

VARIATION – Females sporosacs from Britain may contain up to 15 eggs, hydranths are orange (Jones, 1992). According to Dons (1912) the male sporosacs become ovoid with a pointed distal end when fully mature.

BIOLOGY – Grows on a variety of substrates such as mussels, hydroids, bryozoans, and holdfasts of macroalgae. Depth range 0–100 m.

DISTRIBUTION – Greenland (Kramp, 1914; Schuchert, 2001a), Iceland (Schuchert, 2001a), Spitsbergen (Broch, 1909), White Sea (Antsulevich & Polteva, 1986), Norway (Dons, 1912), British Isles (Jones, 1992), north-eastern Canada (Calder, 1972). Type locality: Bismarck Sound, Spitsbergen, 35 m, on *Grammaria abietina*.

REMARKS – In his first description, Broch (1909) used the specific name *nudum*. In a footnote, Dons (1912) mentioned that Broch had asked him through a letter to change this to *nudus* because the gender of *Rhizogeton* is masculine (“geton” is derived from the Greek word γείτων for neighbour, which is masculine). Following the rules of the ICZN (ICZN, 1999: § 31.2 and 34.2), the specific epithet must have an ending matching the gender of the genus. The correct name is thus *Rhizogeton nudus* Broch, 1909.

Broch (1909) and Dons (1912) described the hydranths as devoid of a basal perisarc. Careful examination with the help of a compound microscope nevertheless revealed the presence of a fine perisarc in the material examined here.

The development of the sporosacs is well documented by the study of Dons (1912).

The sporosacs depicted by Millard (1975) had no pedicels and were directly attached to the stolons. This material from the tropical Indian Ocean as well as the

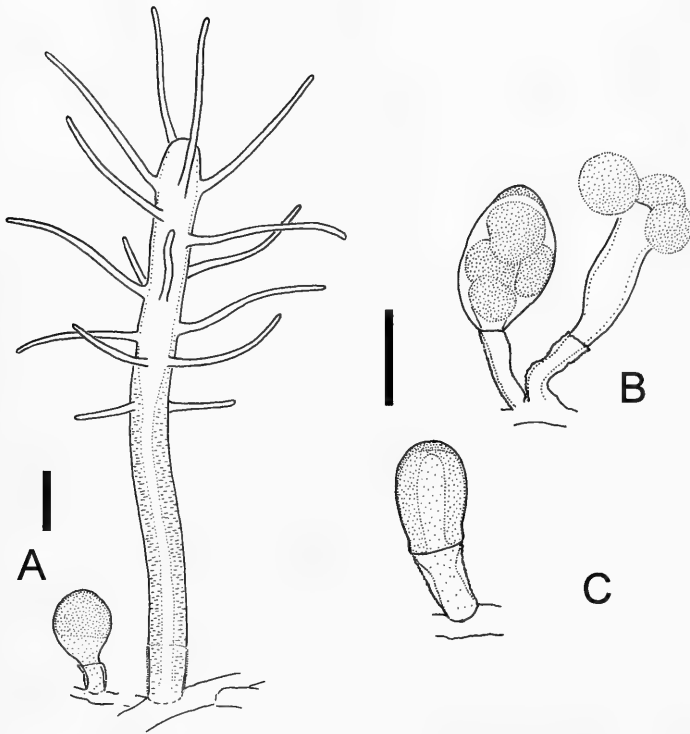


FIG. 9

Rhizogeton nudus Broch, 1909, after preserved material from Iceland (A) and Greenland (B-C). A) Hydranth and presumed gonophore, scale equals 0.3 mm. B) Female sporosacs, right with shed envelope and eggs still sticking to spadix, scale equals 0.5 mm. C) Young male sporosac, same scale as B.

records of Mammen (1963) and Ritchie (1910b) may therefore belong to separate species. Mammen (1963), Rees & Thursfield (1965) and Antsulevich & Polteva (1986) made similar suggestions. The male sporosacs described by Genzano (1993) in material from Argentina likewise lacked a pedicel and may therefore also belong to another species. *Rhizogeton nudus* is probably restricted to arctic and cool-temperate waters of the North Atlantic.

Park (1997) suggested that *R. fusiformis* L. Agassiz, 1862 and *R. nudus* are conspecific. Although Dons (1912) kept both species apart, he found that there is little difference in the morphology of the gonophores. Calder (1988a) re-examined the type material of *R. fusiformis* and he confirmed that this species has a pointed hypostome and only about 10 tentacles. The differences even prompted Calder (1988a) to place the two species in different genera (see remarks under genus *Rhizogeton*). I therefore think that *R. fusiformis* and *R. nudus* of the north-west Atlantic should be kept distinct.

In his report on hydroids of Valencia Harbour (western Ireland), Browne (1897) also described material which he attributed to *R. fusiformis* L. Agassiz, 1862, although he noted marked differences to Agassiz's description. The most critical difference was

the number of tentacles, which was around 20 and not 10-12. The data given by Browne (1897) closely match *R. nudus* as described above and it is very likely that his specimens belonged to this species. This interpretation is supported by the finding of *R. nudus* in the Morecambe Bay (Irish Sea, England; Jones, 1992).

***Cordylophora* Allman, 1844**

TYPE SPECIES – *Cordylophora lacustris* Allman, 1844 by monotypy.

DIAGNOSIS – Erect, branching hydroid colonies, side-branches and hydranth pedicels not adnate, perisarc tubes not nested. Relaxed hydranths spindle-shaped, hypostome well delimited from hydranth body, filiform tentacles scattered in distal half of hydranth body. Gonophores oblong, borne on pedicels of hydranths and on branches, sessile sporosacs with branched spadix.

REMARKS – *Cordylophora* resembles somewhat to the genus *Pachycordyle* and could as well belong to the Pachycordylidae (comp. Morri, 1980; Stepanjants *et al.*, 2000). Unfortunately, there are no convincing synapomorphies that would link it unambiguously to either the Oceanidae or the Pachycordylidae. Mainly for historic reasons, it is here kept in the Oceanidae. It shares with this family the tentacles that are scattered over much of the hydranth body, while in the Pachycordylidae they are concentrated in the distal part.

***Cordylophora caspia* (Pallas, 1771)**

Fig. 10

Tubularia caspia Pallas, 1771: 479.

Tubularia cornea Agardh, 1816: 258.

Cordylophora lacustris Allman, 1844: 330; Allman, 1853: 367, pls 25-26; Schulze, 1871: 1-52, pls 1-6; Hincks, 1868: 16, pl. 3 fig. 2; Allman, 1872: 252, pl. 3; Nutting, 1901: 327, fig. 2; Roch, 1924a: 350, footnote 1.

Cordylophora albicola Kirchenpauer, in Busk, 1861: 284, pl. 9 figs 12-14; Allman, 1872: 254.

Cordylophora lacustris var. *otagoensis* Fyfe, 1929: 813, figs 2-10.

Cordylophora americana Leidy, 1870: 113.

Cordylophora whiteleggi von Lendenfeld, 1886: 97, pl. 6 figs 11-12.

Cordylophora lacustris otagoensis – Ralph, 1953: 64 fig. 6.

Cordylophora caspia – Vervoort, 1946: 119, fig. 47b & 48a (not others); Naumov, 1969: 196, fig. 66; Rossi, 1971: 20, fig. 6I; Morri, 1980: 155, figs 1-3; Morri, 1981: 45, fig. 13, pl. 1 fig. 3, pl. 2 fig. 3; Morri & Boero, 1986: 34, figs 14-15a-b; Barnes, 1994: 60, fig; Holstein, 1995: 95 figs 49-50; Schuchert, 1996: 15, fig. 3a-e.

MATERIAL EXAMINED – MHNG INVE 34179, Rostock, Germany, Baltic Sea (not well preserved, no hydranths left) – ZMUC, Randers Fjord, Møllerup, Denmark, 1.5 m, 25.05.1916 – ZSM, as *C. lacustris*, Elbe estuary, Germany, fertile – ZSM, as *C. lacustris*, Brunsbüttel, Germany, fertile – ZSM, as *C. lacustris*, Woltersdorf near Berlin, Germany, fertile, 3.08.1920 – ZSM, as *C. lacustris*, Heringsdorf, Germany, fertile – ZSM, as *C. lacustris*, Greifswald, Germany, June 1902 – New Zealand, see Schuchert (1996).

TYPE MATERIAL – There presumably exists no type material of *C. caspia*.

DESCRIPTION – Erect, branching hydroid colonies, stems up to 3 cm high (reportedly up to 10 cm), arising from reticulate stolons. Occasional autoepizooism possible. Erect shoots with monopodial growth, branching several times irregularly at various angles, ending in up to 40 hydranths. Shoots often composed of a long main stem and shorter side branches, branches not adnate, stem diameter about 0.2 mm.

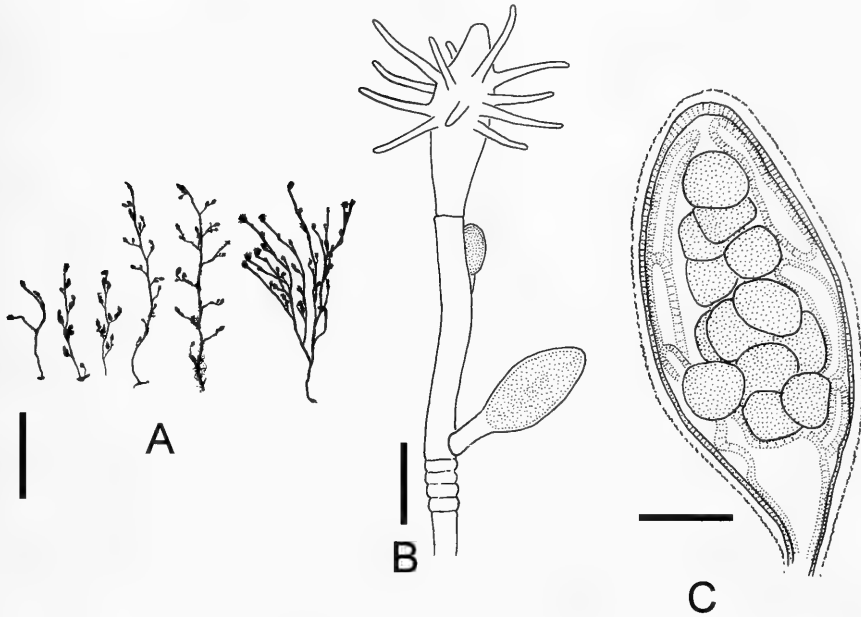


FIG. 10

Cordylophora caspia (Pallas, 1771), A samples from Germany, B-C from Denmark. A) Colony silhouettes demonstrating variability, scale equals 5 mm. B) Hydranth with two gonophores on its pedicel, scale equals 0.2 mm. C) Schematic optical section of a mature female gonophore, eggs are shown stippled and surrounded by solid line, note branched spadix, scale equals 0.2 mm.

Colonies living under unfavourable conditions remain stolonal with hydranths on a simple perisarc covered pedicel. Perisarc smooth with occasional annulated stretches, perisarc ends below hydranths. Relaxed hydranths spindle-shaped, contracted ones ovoid, 1-2 mm high, size variable even within a single shoot, with prominent hypostome, the latter bullet-shaped to conical. Scattered filiform tentacles, usually around 14-16 (up to 27 possible), proximal third of hydranth body free of tentacles. Tentacles of varying length (up to 1.4 mm), tapering slightly to 3/4 of basal diameter, gastrodermis composed of chordoid cells. Colours: hydranths white or pale pink, perisarc brown. Nematocysts: microbasic euryteles and desmonemes. Colonies dioecious. Gonophores ellipsoid, arising at pedicels of hydranths, branches and stems, covered with perisarc, mature about 0.7-1 mm long, diameter about half the length. Initially with a branched spadix, reduced in later development, gametes released through distal hole. Females with 7-16 eggs (fewer also possible), 0.07-0.12 mm in diameter, developing to planulae in situ.

OCCURRENCE – Circumglobal in temperate and subtropical regions, usually in brackish waters as in estuaries, river deltas and lagoons. Absent from fully marine environments. Sometimes penetrating into completely fresh water, but there usually a reduced development. When occurring in inland rivers and lakes, these water bodies

are generally characterized by elevated concentrations of some ions (Arndt, 1984). However, it has recently also been found that *C. caspia* can successfully invade pure freshwater biotopes (Smith *et al.*, 2002). Depth range 0-85 m (Naumov, 1969), usually in very low waters, on rock, under stones, on *Dreissena* spec. (Bivalvia). Type locality: Caspian Sea.

REMARKS ON VARIATION, MORPHOLOGY AND ECOLOGY – There is a vast body of literature on this species and it is impossible to review it here completely. Only the most important works are therefore mentioned. The morphology was studied in detail by Allman (1853), Schulz (1871), and Weismann (1883). The embryology was examined by Van de Vyver (1967). Roch (1924a, 1924b) reviewed all records of this species and examined the influence of chemical and physical parameters on the morphology. These studies were later extended by Kinne (1956, 1957) and Arndt (1984). The morphology of the colony and the hydranths correlates strongly with salinity. Near fresh-water conditions causes low colonies and stolonization, low salinities produce spherical hydranths with short, stubby tentacles, while in water with high salinity hydranths are elongated and their tentacles long and thin. A salinity of 16.7 ‰ at 20 ° and 10 ‰ at 10 °C was found to be optimal for growth in the population examined by Kinne (1957, North Sea to Baltic Sea Channel). Arndt (1984) found a salinity optimum of 6-10 ‰ for populations of the Baltic and Arabian Sea. Sexual reproduction started when water temperatures rose above 10 °C. The temperature optimum was 11-18 °C. Smith *et al.* (2002) found the species in fresh-water and demonstrated that it has successfully invaded this biotope by adjusting its physiology and ecological needs. *Cordylophora caspia* is able to survive long periods without food. This is especially pronounced in fresh water, where it has lived without feeding up to six months (Kinne, 1956). Bouillon (1963) found that this species can be either larviparous or viviparous. For more references see also Holstein (1995), Folino (2000), and Smith *et al.* (2002).

TAXONOMIC REMARKS – Although the original description of *Tubularia caspia* by Pallas (1771) is too vague to allow an unambiguous recognition, most contemporary authors have followed Roch (1924b) in considering it a senior synonym of *C. lacustris* Allman, 1844. Stepanjants *et al.* (2000) disagree, however, without providing arguments. A good review, and remarks on the taxonomic status, can be found in Folino (2000), who also considers the possibility that more than one species might be included in the present concept of *C. caspia*. It is certainly possible that *C. caspia* and *C. lacustris* – the latter referring to populations confined to nearly or fully freshwater conditions – are morphologically inseparable, but nevertheless represent two separate biological species. Genetic methods must be used to clarify the status of the various *Cordylophora* ecomorphs.

Vervoort (1964) examined type material of *Bimeria* (?) *baltica* Stechow, 1923 and found it indistinguishable from *C. caspia*.

PACHYCORDYLIDAE Cockerell, 1911

SYNONYM – Clavopsellidae Thiel, 1962.

DIAGNOSIS – Anthothecata Filifera, polyp phase forming stolonial or branching colonies, hydranths pedicellate, perisarc terminating at base of hydranth, without

pseudohydrotheca. Hydranths club-shaped, spindle-shaped, or amphora-shaped; hypostome nipple- to dome-shaped. Tentacles in two or more whorls restricted to a narrow band below hypostome, spreading over less than one third of the hydranth body only. Gonophores arising on stems or pedicels. Gonophores free medusae, medusoids that can be liberated, or fixed sporosacs. Medusae at liberation with four simple or branched oral tentacles arising above mouth, four tentacle bulbs with one tentacle each, ocelli present.

REMARKS – The family Pachycordylidae comprises the genera *Pachycordyle* and *Silhouetta*. Thiel (1962) proposed the new family Clavopsellidae comprising the genera *Clavopsella*, a synonym of *Pachycordyle*, and *Balella* Stechow, 1919. The latter genus has hydranths with two widely separated whorls of tentacles and it produces gonophores on gonozooids. Schuchert (2003b) argued that *Balella* has closer affinities with the Hydractiniidae and must be placed into a family of its own (Tubidendridae, although the valid name is Balellidae, see Calder 1988a: 13). Thiel was probably unaware that there was already a family group name available that included *Pachycordyle*, namely Pachycordylini Cockerell, 1911. Calder (1988a) raised it to subfamily level as Pachycordylinae and he provided arguments why it must be preferred over Clavopsellidae and why *Silhouetta* should be included in the group. Here, the taxon Pachycordylinae is raised to family level, becoming thus Pachycordylidae. I think this is necessary because *Pachycordyle* is so intermediate between Oceanidae and Bougainvilliidae that it threatens the scope of both families.

The affinities of *Pachycordyle*, or its synonyms *Clavopsella* and *Thieliana*, are disputed even by contemporary authors. Some authors, including Millard (1975), Bouillon (1985), and Calder (1988a), place *Pachycordyle* in the Bougainvilliidae, while Morri (1980) and Stepanjants *et al.* (2000) firmly associate it with *Cordylophora* and the Clavidae sensu Bouillon (1985). To the present author its affinities with the Bougainvilliidae appear to be more evident. *Pachycordyle navis* and *Pachycordyle pusilla* sometimes approach the bougainvilliid species *Aselomaris michaeli* Berrill, 1948 so much, that they could be easily confused. Also, the hydranths of the genera *Parawrightia* Warren, 1907, *Velkovrhia* Matjašič & Sket, 1971 or *Pruvotella* Motz-Kossowska, 1905 are intermediate between *Pachycordyle* and *Bougainvillia*. All of them have two or more whorls of tentacles. Even *Bougainvillia muscus* (Allman, 1863), certainly a typical representative of the Bougainvilliidae, may have two whorls of tentacles, although quite closely approximated (own observations on living Mediterranean material). But most importantly, *Silhouetta uvocarpa* Millard & Bouillon, 1973 has a trophosome identical to that of *Pachycordyle*, but it produces medusae with branched oral tentacles. This definitely indicates a closer relationship to the Bougainvilliidae. The occurrence of nematocysts on the eggs of *Pachycordyle navis* (see Thiel, 1962, as *Clavopsella quadrangularia*) and in many other bougainvilliids as well (Russell, 1953 for *B. macloviana*; Szollosi, 1969 for *B. multitentaculata*; Calder, 1971 for *B. rugosa*; Piraino, 1992 for *A. michaeli*; Calder 1993 for *B. abberans*; Schuchert, 1996 for several species) could be interpreted as a synapomorphy. However, the distribution of such “stinging eggs” (Piraino, 1992) among the Filifera is too insufficiently known to draw a well supported conclusion. The few Oceanidae examined for this study apparently lack a conspicuous nematocyst layer on their egg surface.

Contrary to the view of Calder (1988a), the genus *Millardiana* is not included in the Pachycordylidae because it develops gonophores on the hydranth body (see under family Oceanidae, discussion relating to *Tubiclava*).

The genus *Silhouetta* is thus far not known to occur in the region under investigation, but Cornelius (1992) recorded *Silhouetta uvocarpa* Millard & Bouillon, 1973 from the nearby Azores. Considering its wide occurrence, ranging from the Seychelles to the western tropical Atlantic (Calder, 1988a), it might also occur along the coasts of southern Portugal or Spain.

***Pachycordyle* Weismann, 1883**

SYNONYMS – *Clavopsella* Stechow, 1919; *Thieliana* Stepanjants *et al.*, 2000.

TYPE SPECIES – *Pachycordyle napolitana* Weismann, 1883 by monotypy.

DIAGNOSIS – Stolonal or branching hydroid colonies, hydranths pedicellate, perisarc terminating at base of hydranth. Hydranths club-shaped, hypostome dome- to nipple-shaped, tentacles in two or more close whorls. Gonophores borne on stems or pedicels. Gonophores fixed sporosacs or degenerated pyriform medusae lacking mouth, marginal tentacles, oral tentacles, radial canals, or ocelli.

REMARKS – *Clavopsella* Stechow, 1919 is clearly a junior synonym of *Pachycordyle* Weismann, 1883 (Calder, 1988a; Stepanjants *et al.*, 2000). The definition of *Pachycordyle* adopted in this work follows that used by Thiel (1962) and Millard (1975) for *Clavopsella*. This definition also includes *Pachycordyle navis* and other similar species. Calder (1988a) did not agree with this and considered *P. navis* as belonging to the subfamily Bougainvilliinae rather than the Pachycordylinae and he referred *Pachycordyle navis* to the genus *Aselomaris* Berrill, 1948. Stepanjants *et al.* (2000) again placed *P. navis* in the same subfamily as *Pachycordyle napolitana*, but in the new genus *Thieliana*. *Thieliana* differs from *Pachycordyle* only in the degree of reduction of its gonophores. While *Pachycordyle* sensu Stepanjants *et al.* (2000) has either radial canals or a circular canal, they are absent in *Thieliana*. In the remarks relating to *Pachycordyle napolitana*, I will show that there is probably no real circular canal present in this species. The radial canals of *Pachycordyle kubotai* Stepanjants *et al.*, 2000 are additionally somewhat unusual in that they are not between layers of epidermis. Perhaps they are better homologized with a branched spadix. Generic distinction based on the degree of gonophore reduction have been shown to lead to artificial taxa in many cases (e. g. Petersen 1990, Bouillon *et al.* 1997, Boero *et al.* 1998, Schuchert 2001b). The degree of gonophore reduction, notably if it is only so slight as in the case for *Thieliana*, should therefore not be used to distinguish genera if this trait does not concord with other, independent characters. *Thieliana* is here thus treated as a synonym of *Pachycordyle*.

Kramp (1959, 1968) allocated a number of degenerate medusae to *Pachycordyle*. Kramp himself considered these medusae as possibly belonging to very different taxa and they are placed only temporarily in *Pachycordyle* pending forthcoming information on their polyp phase.

In the region under investigation, there are three known species referable to the genus *Pachycordyle*: *P. napolitana*, *P. navis*, and *P. pusilla*. Piraino (1992) reported

Clavopsella michaeli (Berrill, 1948) from the Mediterranean. This species has a single whorl of tentacles and is here seen as belonging to the Bougainvilliidae. It should therefore not be included in the genus *Clavopsella*, or its senior synonym *Pachycordyle*.

***Pachycordyle napolitana* Weismann, 1883**

Fig. 11

Pachycordyle napolitana Weismann, 1883: 87; Neppi, 1921: 5, fig. 1; Calder, 1988a: 15, figs 11-12.

Cordylophora annulata Motz-Kossowska, 1905: 66, fig. 5; Stechow, 1923: 56.

Perigonimus neapolitanus – Motz-Kossowska, 1905: 75, fig. 8 [incorrect subsequent spelling]. [not *Perigonimus napolitanus* Hargitt, 1904 = *Leuckartiara octona* (Fleming, 1823)].

Pachycordyle weismanni Hargitt, 1904: 553, pl. 21 figs 1-8; Kramp, 1959: 94; Kramp, 1961: 52.

Tubiclava annulata – Stechow, 1912: 343, pl. 13 fig. 8.

? *Tubiclava fruticosa* – Neppi, 1917: 47, fig. 9.

Clavopsella weismanni – Stechow, 1923: 55.

Clavopsella annulata – Wedler & Larson, 1986: 86, fig. 8Aa-f, 9.

? not *Cordylophora neapolitana* – Morri, 1980: 159, figs 4-5; Morri & Boero, 1986: 34, fig. 15c; Morri, 1981: 47, fig. 14, pl. 1 fig. 4 [incorrect subsequent spelling].

MATERIAL EXAMINED – IRSNB, Italy, Naples, young female colony collected by J. Bouillon, June 1962 – ZSM, Stechow collection, as *Clavopsella weismanni* several colonies from Naples collected 1897-1904 as alcohol preparation and slide material, includes male and female colonies, gonophores of variable developmental stages, all colonies on *Fusinus rostratus*.

TYPE MATERIAL – There presumably exists no type material of *P. napolitana*.

DESCRIPTION – Colony stolonal, or rarely pedicels branched once. Pedicels of very varied length (1-15 mm, usually below 5 mm), usually widening distally, bearing a terminal hydranth. Perisarc moderately thin, irregularly corrugated throughout, not distinctly double-layered, terminating at base of hydranth, not forming pseudohydrotheca. Hydranths club-shaped, 1-2 mm long, diameter about 0.3 mm if expanded, when contracted much thicker, in distal third 12-24 tentacles, in larger hydranths distinctly scattered in a broad band (3 whorls), in smaller hydranths more concentrated into a narrow band and almost appearing as one whorl only, proximal tentacles often smaller than distal ones, contracted tentacles filiform, well expanded tentacles moniliform. Hypostome dome- to nipple-shaped. Gonophores arise from hydranth pedicels at some distance below hydranth, 1-3 per pedicel, on short stalk, completely infested with soft, wrinkled, detritus-covered perisarc, shape ovoid, length up to 1.6 mm, diameter 0.8-1 mm. Mature gonophore medusoid, with a distinct subumbrella and a short collar projecting into subumbrella resembling a velum (Fig. 11I). Radial canals absent, circular canal presumably absent. Vestigial manubrium simple, large. Below manubrium a bubble-like gastrodermal chamber (Fig. 11G-I). Gonads encircling manubrium in a thick layer so that it is completely covered. Females with 100-150 eggs, oocytes with relatively large pronucleus, eggs shed and developing free in the water. Egg size about 0.07 mm. Immature male gonophores resembling sporosacs, manubrium large and with pointed diverticulae, mature male sporosacs also medusoid and identical to female ones.

FURTHER DATA – Shoots may have up to three hydranths (Weismann, 1883). Hydranth body orange or reddish, hypostome whitish (Hargitt, 1904). Nematocysts are microbasic euryteles and desmonemes (Calder, 1988a).

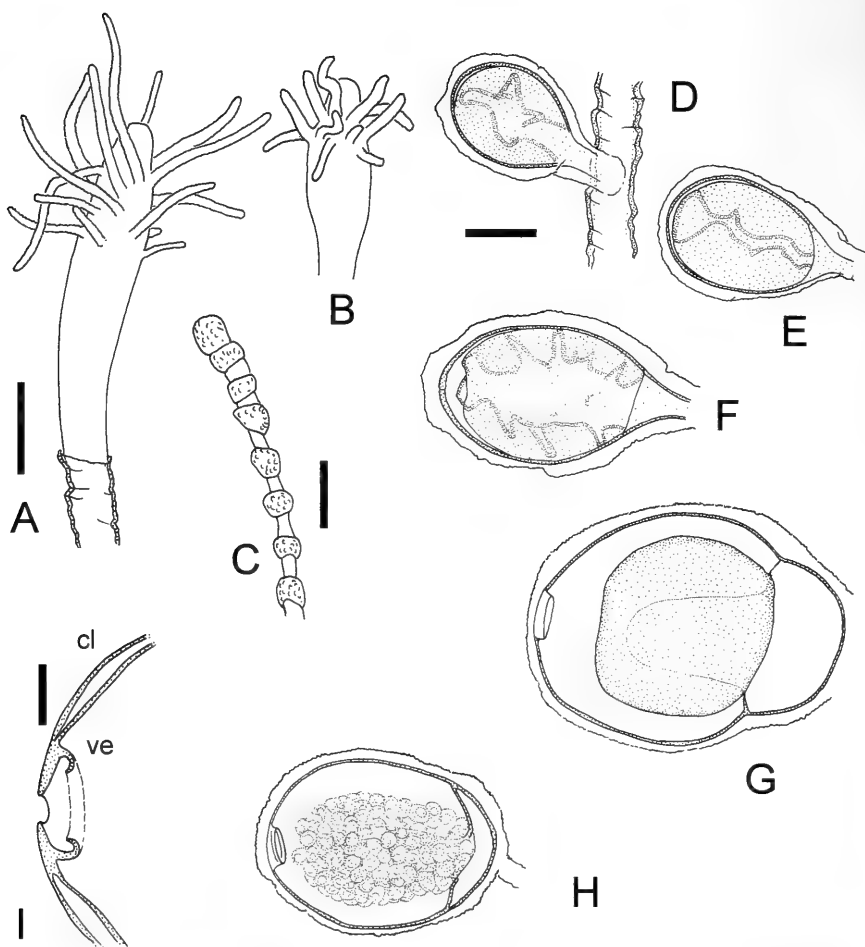


FIG. 11. *Pachycordyle napolitana* Weismann, 1883, after preserved material from Naples. A) Hydranth with somewhat contracted tentacles, scale equals 0.4 mm. B) Hydranth, note that tentacles are less scattered than in specimen shown in A, same scale as A. C) Tip of a fully expanded tentacle, note moniliform arrangement of nematocyst clusters, scale equals 50 μ m. D-F) Successive developmental stages of a male gonophore, note branched spadix (manubrium), scale equals 0.3 mm. G) Fully mature male medusoid, it is still enveloped by perisarc film, same scale as D. H) Mature female medusoid, note that there is no more tissue connection to the polyp stage, but the medusoid is still within the perisarc envelope, same scale as D. G) Higher magnification of the distal opening of the female medusoid, ve = velum-like collar, cl = cleft, a possible fixation artefact and likely not a circular canal, scale equals 0.1 mm.

BIOLOGY – Reliable identifications are from fully marine conditions only. Colonies usually grow on gastropod shells (*Fusinus rostratus*, *Murex* spec.), either inhabited by mollusc or hermit crabs, mostly on muddy bottoms; known to occur in depths from a few metres to perhaps 40 m; mature from spring to October. Boero & Fresi (1986) also found it growing on algae and *Eudendrium* spec. (fully marine conditions).

DISTRIBUTION – Western Mediterranean (Weismann, 1883; Hargitt, 1904; Motz-Kossowska, 1905; Lo Bianco, 1909; Stechow, 1919; Neppi, 1921; Stechow, 1923; Boero & Fresi, 1986), Adriatic Sea (Stechow, 1912), Bermuda (Calder, 1988a), Puerto Rico (Wedler & Larson, 1986). Type locality: Mediterranean, Naples, 40 m, on empty *Murex* shell.

REMARKS – Weismann (1883) described *P. napolitana* only summarily, as he was more interested in its histology and in the development of the gonophores. The gonophores he described were male, appeared like sessile sporosacs, and had a characteristic, branched spadix. Hargitt (1904), also studying material from Naples, found similar colonies which were all female. Although he noted the close resemblance to *P. napolitana*, he assigned his material to a separate species and named it *P. weismanni*, based mainly on the medusoid gonophores he observed. Shortly afterwards, Motz-Kossowska (1905) published her findings of athecate hydroids from the western Mediterranean. Motz-Kossowska, most probably unaware of Hargitt's publication, also described a new species with several whorls of filiform tentacles and female medusoid gonophores and named it *Cordylophora annulata*. A similar, male colony with sporosacs identical to Weismann's material was allocated by her to *P. napolitanus* under the name *Perigonimus neapolitanus* (Weism.) (not to be confounded with *P. neapolitanus* Hargitt, 1904, presumably a synonym of *Leuckartiara octona*). Mayer (1910) concluded that *P. napolitana* and *P. weismanni* belonged to the same species and that the differences of the two nominal species were attributable only to differences of the sex. Neppi (1921) put forward the same thoughts and substantiated this by observations. She demonstrated that the male gonophores of *P. napolitana* are also medusoid and have intermediate developmental stages resembling those described by Weismann. Stechow (1923) vehemently rejected the idea of Mayer and insisted that *P. napolitana* and *P. weismanni* are separate species. Additionally, he also kept *C. annulata* distinct from *P. weismanni*, although without giving arguments. A re-examination of Stechow's material, today kept by the ZSM, makes it difficult to understand Stechow's opinion, as the material clearly shows several developmental stages of male gonophores (Fig. 11D-G). It is especially important to note the development of the spadix, which initially has very characteristic lateral diverticulae, resembling a branched spadix (Fig. 11F). Such a spadix was also described by Weismann (1883). There can thus be no doubt that *C. napolitana* and *P. weismanni* are conspecific, although they were initially recorded on different gastropod shells (*Murex* spec. versus *Fusinus rostratus*). Thiel (1962) continued to use *P. weismanni*, and he kept *P. annulata* Motz-Kossowska, 1905 separate on account of the absence of a circular canal and the different branching degree, although Motz-Kossowska did not explicitly mention the absence of such a ring canal. Hargitt (1904) made histological sections of the medusoids and found a cleft-like space encircling the bell opening which he interpreted as a circular canal, although it lacked an epithelial lining. In the slide material made by Stechow, a similar cleft can be seen (Fig. 11I), but it is very likely that it is only a fixation artifact as in Hargitt's material. Thus, *Pachycordyle napolitana* very likely has no real circular canal.

Pachycordyle napolitana has usually been reported growing on gastropod shells in waters of normal salinity, both in the Mediterranean and elsewhere (Wedler &

Larson, 1986, as *C. annulata*; Calder, 1988a). Boero & Fresi (1986) recorded it also on algae and *Eudendrium* spp., also in a fully marine environment. Morri (1980, 1981) reported *P. napolitana* on seagrasses growing in brackish waters. It seems, however, that medusoid gonophores were never observed in these animals (see comment in Morri, 1980: 163). Because this is an essential character in distinguishing them from other similar species, like *P. navis* (Millard, 1959) (see Stepanjants *et al.*, 2000), I think that the identity of Morri's material is not reliably established and needs confirmation. The difference of biotopes – fully marine versus reduced salinity and different substrata – are also arguments for two different species being involved. *Pachycordyle navis* is quite similar and is well known to occur in brackish waters.

As already noted by Stechow (1923), the tentacles in fully grown hydranths of *P. napolitana* are clearly arranged in several whorls, but this may not be the case in smaller or younger hydranths. In preserved and contracted material it can also be quite difficult to recognize more than one tentacle whorl.

Hargitt (1904) observed in aquarium cultures that the mature gonophores are released as free medusoids. As noted by Stechow (1923), this may not necessarily be the case under natural conditions, and some gonophores may spawn even while still attached to the hydranth.

***Pachycordyle navis* (Millard, 1959) comb. n.**

Fig. 12

Rhizorhagium navis Millard, 1959: 244, fig. 2.

Clavopsella quadranularia Thiel 1962: 228, figs 1-28; Schönborn *et al.*, 1993: 217, pl. 2 fig 3.

Corydendrium dispar – Rasmussen, 1973: 22.

[not *Corydendrium dispar* Kramp, 1935].

Clavopsella navis – Millard, 1975: 100, fig. 3A-D.

? *Cordylophora neapolitana* – Morri, 1980: 159, figs 4-5; Morri & Boero, 1986: 34, fig. 15c;

Morri, 1981: 47, fig. 14, pl. 1 fig. 4.

[not *Pachycordyle napolitana* Weismann, 1883].

Cordylophora inkermanica Marfenin, 1983: 1732, fig'd; Stepanjants *et al.* 2000: 226.

Thieliana navis – Faasse & Vervoort, 2001: 181, figs 1-3.

TYPE MATERIAL EXAMINED – Type of *Clavopsella quadranularia* Thiel, 1962, Zoological Museum Hamburg, registration number C7434, loc. Kiel, Aussenhafen, Holtener Schleuse. The type material of *P. navis* is kept by the South African Museum in Capetown, but was not examined during this study.

OTHER MATERIAL EXAMINED – Material described by Rasmussen (1973) as *Corydendrium dispar*; Denmark, Isefjord, on *Mytilus* in the strong currents of the intake of the power station Kyndbyværket, fertile female, material kept by "The Isefjord Laboratory" at Vellerup Vig (University of Roskilde, Denmark), part of this material also deposited as MHNG INVE 34226.

DESCRIPTION – (After Thiel, 1962 and examined material) Colony stolonial or variably branched, height 7-30 mm, 1-30 hydranths per shoot. Stolons ramified, initially creeping on substrate, in larger colonies detached and forming tangled masses, sometimes also growing along stems of older shoots. Pedicels and stems covered by perisarc, terminating below hydranth. Perisarc mostly smooth, some annulated stretched in European colonies. Perisarc often double-layered, inner layer may be annulated while outer layer is smooth (Fig. 12C). Pedicel length variable but relatively long, diameter 0.1-0.15 mm. Hydranth body 1.0-1.8 mm high (1.4 mm mean), diameter about 0.35 mm, spindle-shaped. Hypostome high, dome-shaped. Tentacles 12-24, in a

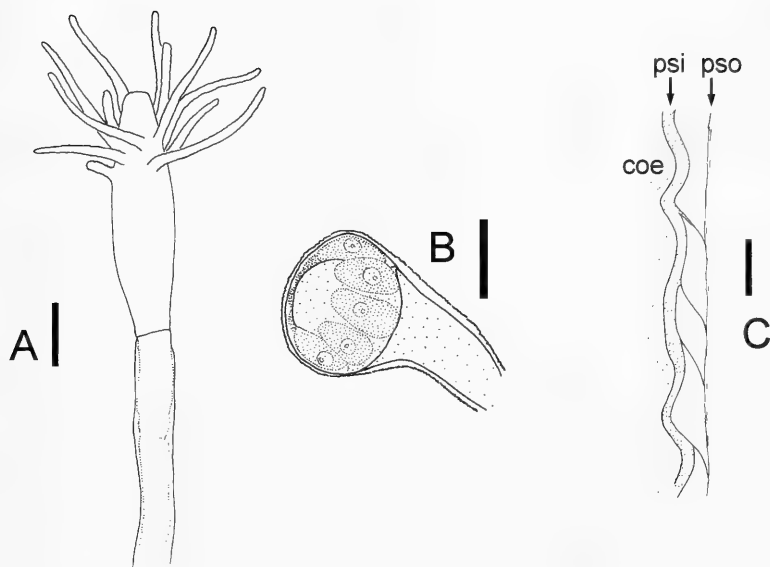


FIG. 12

Pachycordyle navis (Millard, 1959), A-B, after type material of *Clavopsella quadranularia*; C, after material from Denmark. A) Hydranth with part of pedicel, scale equals 0.2 mm. B) Female sporosac, scale equals 0.2 mm. C) Higher magnification of double-layered perisarc, coe = coenosarc, psi = inner perisarc layer, psa = outer perisarc layer, note the thin lamellae connecting both layers, scale equals 50 μ m.

narrow band below hypostome, 2-4 closely approximated alternating whorls. Gonophores about 0.4 mm, borne in irregular spiral on stem or hydranth pedicels. Gonophores with relatively long pedicel, completely sheathed in perisarc. Gonophores fixed sporosacs (heteromedusoids) with distinct spadix, lacking tentacle rudiments, radial canals, circular canal, or velum. Colonies dioecious. Male sporosacs spherical to spindle-shaped. Female sporosacs club-shaped, distal end obtuse, containing a very variable number of eggs, 5-20, if up to 12 eggs then these in one tier, but arrangement can also be irregular, eggs about 0.1 mm in diameter, covered with a few nematocysts only. Eggs develop into planulae in situ. Nematocysts: microbasic euryteles, desmonemes. Colour: perisarc clear to brown, coenosarc white to reddish, hydranths red (depends on food).

BIOLOGY – Euryhaline. European colonies known from brackish waters only, the minimal salt concentration is perhaps 8 ‰; experimental cultures in seawater of normal salinity kept well over long time (Thiel, 1962). The South African colony was growing on a ship hull that had never left South Africa. Grows on algae, wood, iron constructs, *Mytilus*, and other solid substrata. Thiel (1962) observed two periods of reproductive activity: in spring and late summer to autumn.

DISTRIBUTION – South Africa (Millard, 1975), Baltic Sea (Thiel, 1962, as *C. quadranularia*), southern England (Barnes, 1994), The Netherlands (Faasse & Vervoort, 2001), Denmark (this study), Black Sea (Marfenin, 1983, as *Cordylophora inkermanica*). Type locality: Table Bay, South Africa, on hull of ship.

REMARKS – This species was initially described as *Rhizorhagium navis* Millard, 1959. Later Millard (1975) placed it in the genus *Clavopsella*. Because *Pachycordyle* Weismann, 1883 has priority over *Clavopsella* Stechow, 1919, this species is here referred to the former genus as *Pachycordyle navis* (Millard, 1959) new comb.

Millard (1975) reported that she had compared material of *P. navis* with Thiel's *Clavopsella quadrangularia* and both authors agreed that they were very likely conspecific.

As put forward by Stepanjants *et al.* (2000), *Cordylophora inkermanica* Marfenin, 1983 appears indistinguishable from *P. navis* and it is here regarded as a synonym of the latter.

Material identified by Rasmussen (1973) as *Corydendrium dispar* was re-examined during this study. Although not well preserved, it is obviously referable to *P. navis*. Some preserved hydranths have the typical tentacle arrangement of this species. The side branches arise at acute angles, but remain not adnate as in *C. dispar*. Also, the well preserved female sporosacs were rather typical. The double-layered perisarc seen in both *C. dispar* and *P. navis* may have mislead Rasmussen to identify his material as *C. dispar*.

Pachycordyle navis resembles *P. pusilla* Motz-Kossowska, 1905, but the latter is smaller, is stolonal, has fewer eggs per sporosac, and has a funnel-shaped perisarc dilation at the distal end of the pedicel. Furthermore, their ecology is different, with *P. pusilla* occurring only on sea-grasses in fully marine environments. European records of *P. navis* are all from sites with reduced salinities. There is an interesting similarity in the structure of their perisarc (comp. figs. 12C and 13D). The perisarc is often doubled with a thicker, corrugated inner layer and a thin outer layer. Both layers are connected by thin lamellae. In *P. pusilla*, this double layered-structure is confined to the distal part of the pedicels.

***Pachycordyle pusilla* (Motz-Kossowska, 1905) comb. n.**

Figs 13 & 14

Cordylophora pusilla Motz-Kossowska, 1905: 63, fig. 4, pl. 3 fig. 3-9; Morri, 1980: 164, fig. 6;

Boero, 1981: 188, fig. 2; Schuchert 2003a: 540, fig'd.

? *Pachycordyle fusca* Müller, 1913: 357, figs 3-7, figs 14-23.

Tubiclava pusilla – Stechow, 1919: 10; Leloup, 1930: 24, figs 1-3.

Merona pusilla – Picard, 1951: 349.

TYPE MATERIAL EXAMINED – ZSM, syntype material of *Pachycordyle fusca*, Stechow collection, one slide labelled as “*Clavopsella* (*Pachycordyle*) *fusca* (H. G. Müller) Neapel Cotypus !” (cotypus in red ink), 2 hydranths with young gonophores (stage 1 acc. Müller, 1913: 399), gastrodermal zooxanthellae clearly visible. The type material of *P. pusilla* could not be located.

OTHER MATERIAL EXAMINED – IRSNB, Mediterranean, Monaco, coll. E. Leloup 1929, on *Posidonia oceanica* (material of Leloup, 1930) – IRSNB, Mediterranean, Villefranche-sur-Mer, coll. E. Leloup 24 Mar 1934, depth 15 m, on *Posidonia oceanica* – ZSM, Naples, as *Clavopsella fusca*, coll. Bedot no. 186, on *Cymodocea nodosa*, with young gonophores – ZSM, as *Clavopsella fusca*, Naples, coll. Spletstösser, fertile females – MHNG INVE 32953, Banyuls-sur-Mer, on *Posidonia oceanica*, 10 May 2002, examined alive, fertile female.

DESCRIPTION – Colony stolonal or rarely branched once, stolons creeping, smooth, mostly linear, growing on seagrasses. Hydranths pedicellate, pedicel 0.4-2 mm high, with perisarcular sheath, perisarc annulated in lower region, at distal end often

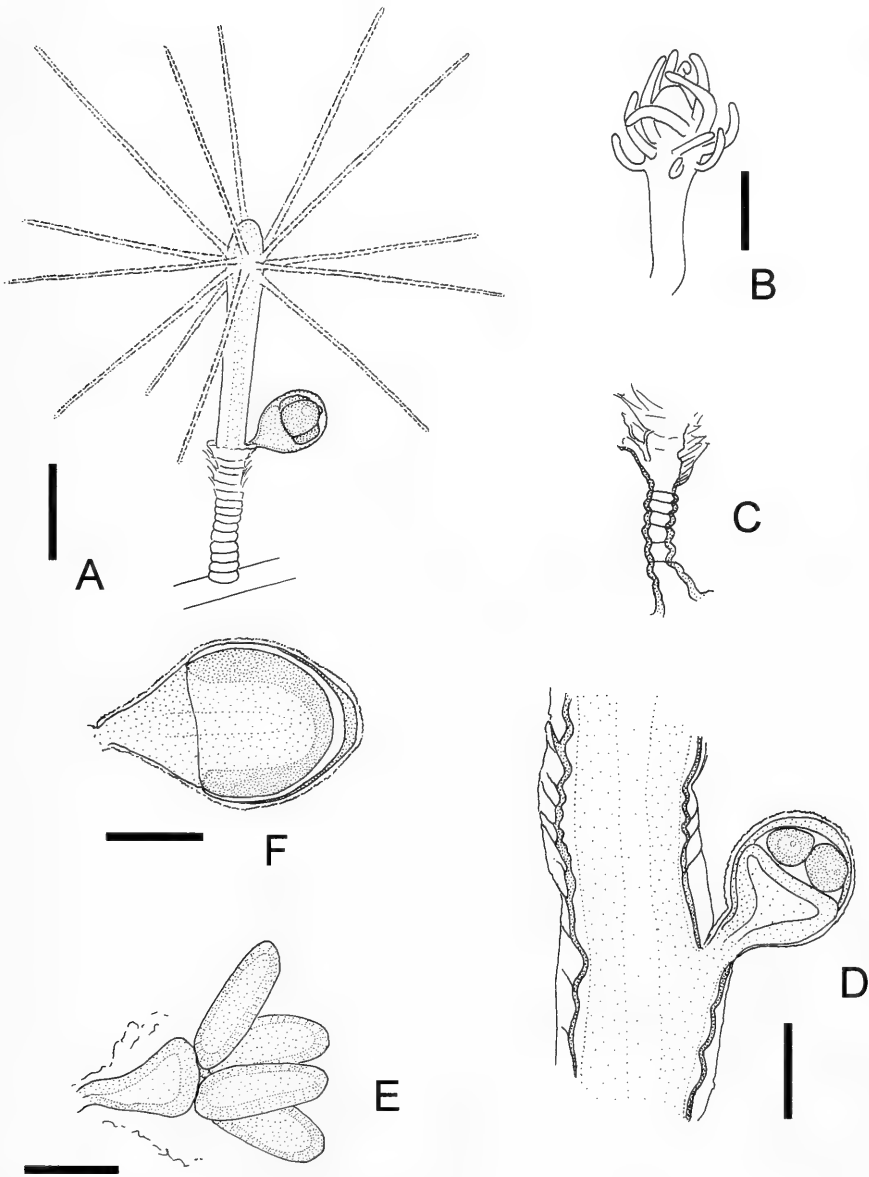


FIG. 13

Pachycordyle pusilla (Motz-Kossowska, 1905). A) hydranth with female sporosac, drawn after living material from Banyuls-sur-Mer, scale equals 0.4 mm. B) Hydranth with contracted tentacles, note scatter of tentacles, preserved material from Monaco, scale equals 0.4 mm. C) Optical section of hydranth pedicel, note double-layered, lamellar structure of distal end, same scale and material as in B. D) Optical section of hydranth pedicel with young female sporosac, preserved material from Naples, scale equals 0.2 mm. E) Final developmental stage of female sporosacs with three fully developed planulae, same material as D, scale equals 0.2 mm. F) Male sporosac in optical section, preserved material from Villefranche, scale equals 0.1 mm.

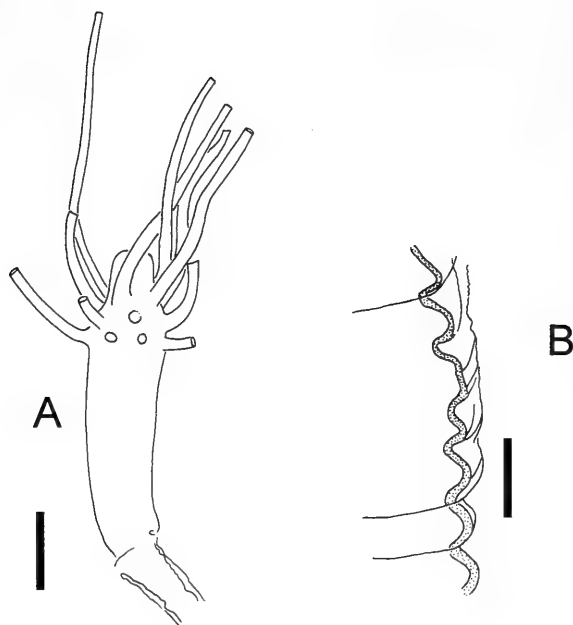


FIG. 14

Pachycordyle fusca Müller, 1913, after type material. A) Hydranth, some tentacles are broken off, note their scattered arrangement, scale equals 0.2 mm. B) Higher magnification of pedicel perisarc in optical section, note annulation and double-layered periderm, the inner thicker and the outer layer are connected by lamellae, scale equals 50 μ m.

expanding and fuzzy, double-layered, the two layers connected by lamellae (Figs 13D), sometimes resembling nested funnels. Hydranth 0.7-1.2 mm, fully relaxed hydranths slightly club-shaped with swelling in region of tentacles (Fig. 13A), hypostome high, dome-shaped. Tentacles radiating from a narrow band below hypostome, 12-16 in number, either in 3 whorls or scattered, expanded very thin, up to 1.4 mm long. Size of tentacle-bearing region quite variable, in some hydranths very narrow, giving the impression of only one whorl being present. Gonophores borne on the hydranth pedicels, usually near the distal end, 1-4 per pedicel. Gonophores sessile sporosacs, without radial or circular canals, no velum, simple spadix present, proximal gastrodermal chamber large, taking up almost the same volume as the gametes. Gonophores surrounded by loose, thin periderm. Females with 4, occasionally 5, eggs in a single tier, eggs uncoloured, clear. Development takes place in sporosacs, planulae remain attached to spadix even after periderm casing has been shed. Nematocysts: microbasic euryteles and desmonemes.

BIOLOGY – Grows on *Posidonia oceanica* or *Cymodocea nodosa* in sea water of normal salinity. Mature colonies found from June to August (Motz-Kossowska, 1905), March to April (Leloup, 1930), October (Boero & Fresi, 1986). Reproduction leads to reduction of hydranths (reproductive exhaustion; Leloup, 1930).

DISTRIBUTION – Mediterranean. Records: Banyuls-sur-Mer (Motz-Kossowska, 1905); Marseille (Stechow, 1919); Monaco (Leloup, 1930); Algeria (Picard, 1955); Genoa (Boero, 1981; Boero & Fresi, 1986); Cabo de Creus, Spain (Gili & Castello, 1985). Type localities: *Pachycordyle pusilla*, near Arago Laboratory, Banyuls-sur-Mer, France, Mediterranean, on *Posidonia oceanica*; *Pachycordyle fusca*, Bay of Naples, on *Cymodocea nodosa*, 2-4 m.

REMARKS – Contemporary authors placed this species in the genus *Cordylophora*. The tentacle arrangement, however, is identical to that of *Pachycordyle napolitana* and *P. navis*. All three species resemble each other quite closely, although they are certainly distinguishable. Therefore, this species is here used in the new combination *Pachycordyle pusilla* (Motz-Kosowska, 1905).

Most hydranths have their tentacles scattered in a band below the hypostome, but in some hydranths they are so close that they can be taken as one whorl only. These polyps look very much like bougainvilliid hydranths.

Motz-Kossowska (1905) mentioned that the eggs are covered by nematocysts. In the examined material from Banyuls, though, only very few nematocysts were present on the egg surface.

Zooxanthellae could not be detected reliably in the examined living hydranths, but they may have been present in low numbers.

Pachycordyle fusca Müller, 1913 very much resembles *P. pusilla* in all aspects, but its gastrodermal tissue contains many zooxanthellae. The zooxanthellae give the hydranth a brown colour. The species has apparently not been mentioned by other authors since its original description. Müller (1913) described *P. fusca* quite precisely, especially the gonophores and their development. In one respect, however, he might have been wrong: the tentacles are not in a single whorl as shown in his figure (Müller 1913: fig. 3). The ZSM collection contains a slide that is very likely syntype material because it is clearly labelled "Cotypus". It was presumably donated by Müller to Stechow, who initiated the hydroid collection of the ZSM (these authors must have been in contact because they also published together, e. g. Stechow & Müller, 1923). This slide preparation contains two hydranths that clearly match Müller's figure, including the double layered perisarc (Fig. 14B). The tentacles, however, are clearly in three whorls (see Fig. 14A). The zooxanthellae are visible in the preparation. Besides the zooxanthellae, and perhaps the host plant, there is thus nothing that distinguishes *P. fusca* reliably from *P. pusilla*, and I suspect that both are conspecific. *Pachycordyle fusca* is therefore listed as a questionable synonym of *P. pusilla*.

Müller (1913) primarily investigated the development of the gonophores and the regeneration of the hydranths and gonophores. He also kept his colonies in the dark which considerably reduced the zooxanthellae, but which had no adverse effect on the hydroid.

Picard (1955) identified hydroids as *Cordylophora pusilla* that were growing on *Cymodocea*. He noted that the gastrodermis contained a small number of zooxanthellae.

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Redescription of *Ophiotaenia hylae* Johnston, 1912 (Eucestoda: Proteocephalidea), parasite of *Litoria aurea* (Amphibia: Hylidae) from Australia

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Redescription of *Ophiotaenia hylae* Johnston, 1912 (Eucestoda: Proteocephalidea), parasite of *Litoria aurea* (Amphibia: Hylidae) from Australia. - Type material of the proteocephalidean cestode *Ophiotaenia hylae* Johnston, 1912 is redescribed. It is characterised by a globular scolex with uniloculate suckers, a prominent apical organ covered by spiniform microtriches and containing round to oblong cells of finely granular cytoplasm, and by the internal longitudinal musculature composed by 4-5 dorsal and 4-5 ventral bundles of fibres. A similar taxon, *Ophiotaenia* sp. from a closely related host species, *Litoria moorei*, is also studied and compared.

Key-words: Eucestoda - Proteocephalidea - *Ophiotaenia hylae* - *Litoria aurea* - *Litoria moorei* - Hylidae - Australia.

INTRODUCTION

Since its original description in 1912, nobody made a redescription of *O. hylae*. Prudhoe & Bray (1982, p. 33, figs 8a, b, c) only published drawings of *Ophiotaenia hylae* (BMNH 1968.4.19.1-15) from *Litoria (Hyla) moorei*, Cannington, Australia. This material has been examined and is here considered as belonging to *Ophiotaenia* sp. (see below) and not to *O. hylae* Johnston. New material of the true *O. hylae* was unavailable due to the extreme scarcity of its host, *Litoria (Hyla) aurea*. This species is actually considered threatened with extinction in Australia (Pyke *et al.*, 2002; Pyke, 2002). I had the opportunity to study Johnston's type material deposited in different Australian museums (Queensland Museum, Brisbane; South Australian Museum, Adelaide). This allowed me to redescribe this material, to add new information to the original description and clarify its taxonomic status.

MATERIAL AND METHODS

The worms, conserved in museum collection in alcohol, were stained with Weigert's haematoxylin solution, dehydrated in an ethanol series, cleared with Eugenol (clove oil), and mounted in Canada balsam. Pieces of strobila were embedded in paraffin wax, cross sectionned (thickness 12-15 μ m), stained with Weigert's haema-

toxylin and counterstained with 1% eosin B according to the method recently published by de Chambrier (2001). All measurements are given in micrometres unless otherwise stated.

Abbreviations used in descriptions: \bar{x} = mean, n = number of measurements, CV = coefficient of variability (%), OV = ovary width to proglottis width ratio, PG = position of the genital pore in relation to proglottis length (%), PC = cirrus pouch length to proglottis width ratio (%), JNT = Johnston original description; BMNH = Natural History Museum, London; MHNG = Natural History Museum, Geneva; INVE = Geneva Museum, Invertebrates Collection; SAM = South Australian Museum, Adelaide; QM = Queensland Museum, Brisbane.

RESULTS

Ophiotaenia hylae Johnston

Figs 1-6

Ophiotaenia hylae Johnston, 1912: 63.

Batrachotaenia hylae; Rudin, 1917: 366.

Batrachotaenia hylae; Freze, 1965: 385.

Type host: *Litoria aurea* (Lesson, 1829) (Amphibia: Hylidae).

Material studied: Syntype material of *Ophiotaenia hylae*: 1 slide V 4141 (SAM 44141); S 689 (SAM 20689), four slides: a) 2 immature pieces, one with scolex; b) 1 immature piece, 9 mm; c) 1 gravid proglottis, 1 mm, bad conservation state; d) 11 gravid proglottides, 15 mm. One immature specimen with a scolex, G 16/423, QM, from *Hyla aurea*, Sydney, NSW, 37°41'S, 144°40'E. Other material: In one separate box containing a lot of Johnston's original material, 1 slide with 12 immature pieces, with one scolex, SAM 28407.

Site of infestation: Intestine.

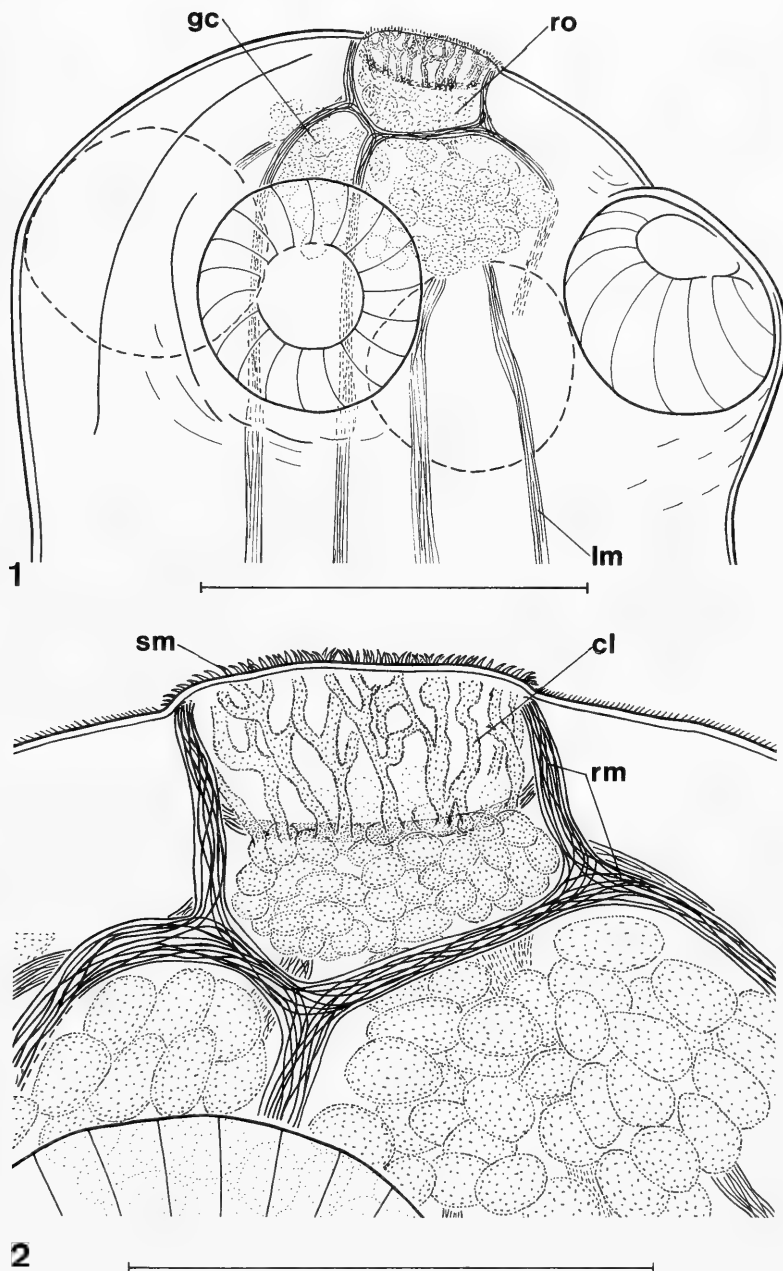
Type-locality: Neighbourhood of Sydney, NSW, Australia.

REDESCRIPTION (based on syntypes and Johnston's original material)

Proteocephalidea, Proteocephalidae. Testes, ovary, uterus diverticles in medulla, uterine stem cortical. In the whole mounted syntype material, one fragment 18 mm long. Strobila acraspedote, anapolytic, consisting of 33 immature and mature proglottides (JNT = 60 mm long). Immature proglottides 540-635 long and 405-500 wide, mature proglottides 695-750 long and 710-865 wide, gravid proglottides 1250-1540 long and 865-920 wide (Figs 3, 4). Tegument thick and wrinkled in mature proglottides. Presence of numerous small dorso-ventral muscles.

Scolex 340-390 (JNT = 320) in diameter (Figs 1-2), covered by small dense microtriches about 1 long, suckers 130-135 (JNT = 110) in diameter. Apical organ, 65-80 in diameter, covered by small dense spiniform microtriches 2-3 long (Fig. 2) above a network of small and poorly defined canals filled with a granular content, and ending beneath tegument surface. Presence of small retractor musculature at the margin of the apical organ (Fig. 2). Beneath the apical organ, a concentration of cells with a finely granular cytoplasm is present in two zones, one just beyond the apical organ and another made of twice bigger cells situated at the level of the suckers (Fig. 2). Longitudinal internal musculature dense, formed by 4-5 thick bundles of fibres on both dorsal and ventral sides (Fig. 5).

Ventral and dorsal osmoregulatory canals between vitelline follicles and testes, crossing cirrus pouch at level of its two-third part (Fig. 3). Ventral canal, twice the



FIGS 1-2

Ophiotaenia hylae Johnston, 1912. Syntype, 20689 SAM. 1. Scolex, general view. 2. Detailed view of the apical organ region. *Abbreviations:* cl, small canals- filled with granular content; gc, gland cells; lm, internal longitudinal musculature; rm, retractator muscles; ro, rostellum-like apical organ; sm, spiniform microtriches (hooklets). Scale-bars: 1 = 200 μ m; 2 = 100 μ m.

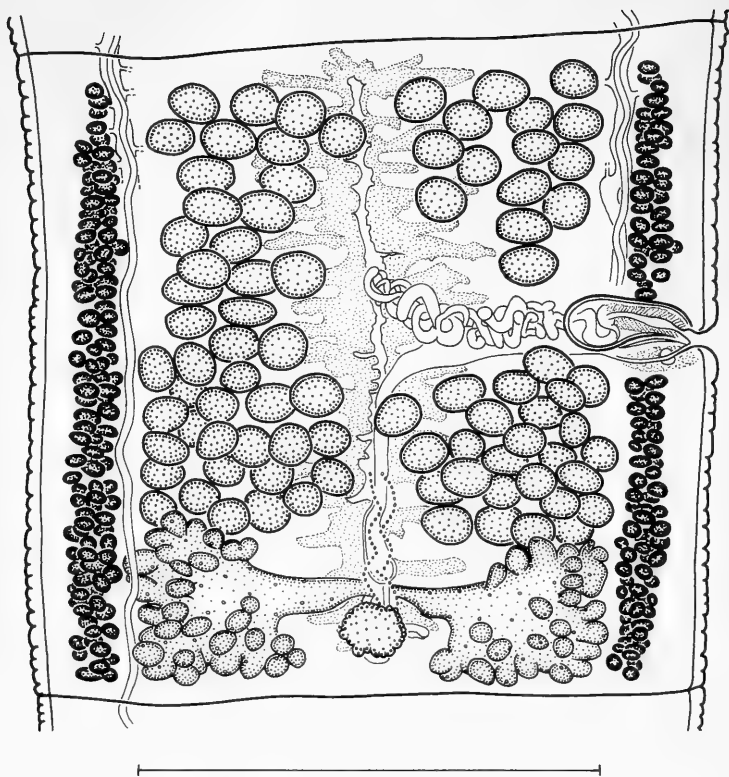
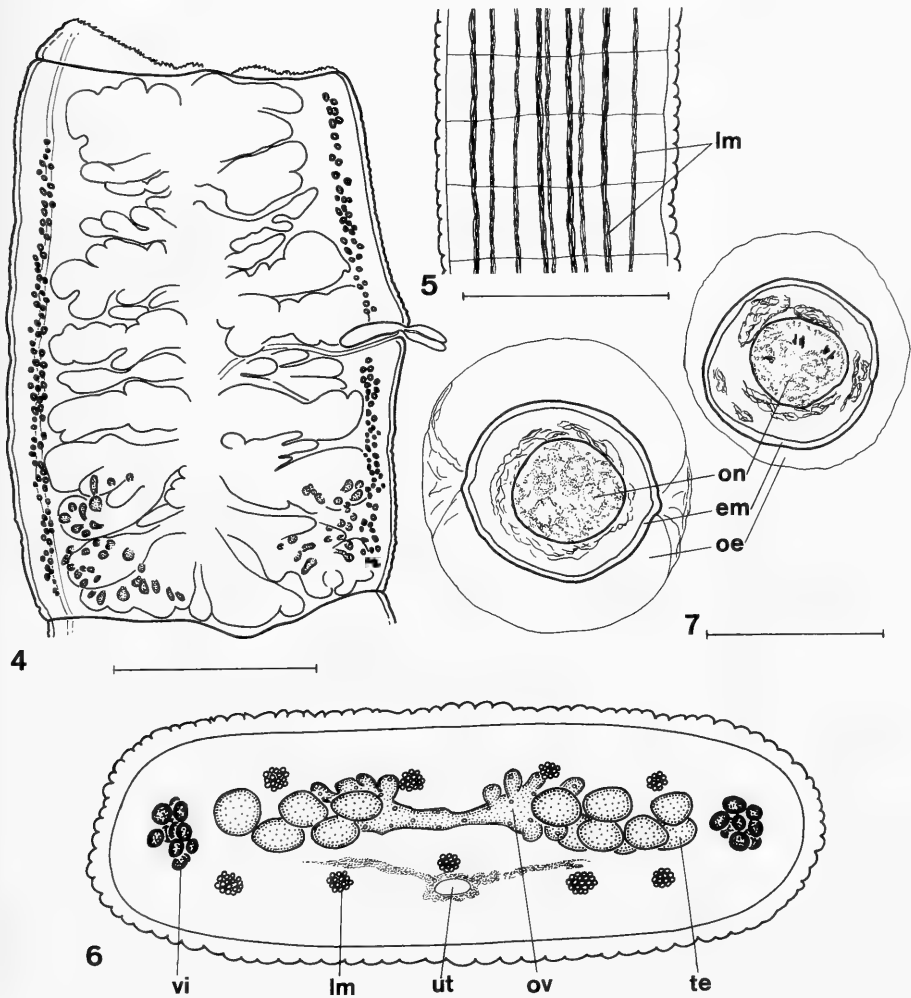


FIG. 3

Ophiotaenia hylae Johnston, 1912. Syntype, 44141 SAM, dorsal view of a mature proglottis. Scale-bar: 500 μ m.

diameter of the dorsal canal, with narrow secondary canals directed externally ventrally. Testes 74-106 in number (\bar{x} = 86, n = 12, CV = 13%, JNT = numerous) in two dorsal field, with tendency to converge anteriorly and posteriorly, in one or two layers dorsally, not reaching laterally to vitelline follicles (Fig. 3), 35-60 in diameter. Testes 15-22 preperal, 16-25 postperal and 38-53 aporal in number. Testes degenerated in gravid proglottides (Fig. 4).

Genital pores irregularly alternating, opening between 44 and 55 % (n = 12, CV = 7%) of proglottis length. Small genital atrium present. Cirrus pouch pyriform, 115-145 long (JNT 140). PC = 17-19% (\bar{x} = 18%, n = 11, CV = 5%). Cirrus occupying up to 70% of cirrus pouch length. Evaginated cirrus covered by numerous minute spiniform microtriches, 2-3 long. Vagina anterior (38%) or posterior (62%) to cirrus pouch (JNT = antero-ventrally), with a small subterminal vaginal sphincter (Fig. 3). When anterior, passing ventrally to the cirrus pouch. Mehlis glands 60-85 in diameter. Vas deferens coiled, between base of cirrus pouch and median part of proglottis, rarely extending beyond body midline in mature and premature proglottides, extending anteriorly.



FIGS 4-7

4-6. *Ophiotaenia hylae* Johnston, 1912. Syntype material, 20689 SAM. 4. Scheme of dorsal view of a gravid proglottis showing the uterine diverticle development. 5. Scheme of the internal longitudinal musculature at level of immature proglottides. 6. Scheme of a cross section showing the disposition of genital organs related to the internal longitudinal musculature. 7. *Ophiotaenia* sp. from *Litoria moorei*. BMNH 1968.4.19.1-15, eggs drawn in distilled water. Abbreviations: em, embryophore; lm, internal longitudinal musculature; oe, outer envelope; on, oncosphere; ov, ovary; te, testes; ut, uterus; vi, vitellaria; Scale-bars: 4 = 500 μ m; 5 = 250 μ m; 6 = no scale; 7 = 20 μ m.

Ovary bilobate, medullary, folliculate, with numerous dorsal outgrowths (Figs 3, 7). OV = 68-71% (\bar{x} = 70%, n = 11, CV = 2%). Vitelline follicles, in two lateral bands, occupying porally 91-97% of proglottis length, and aporally 94-97% of proglottis length (Fig. 3).

Primordium of uterine stem cortical, already present in immature proglottides, with diverticles in medulla. Formation of uterus of type 2 (see de Chambrier *et al.*, 2004): in immature proglottides, chromophil cells concentrated laterally on both sides of uterine stem; in the first mature proglottides, lateral ramified digitations without a lumen, occupying at this stage already about 35% of proglottis width; in gravid proglottides, lateral diverticles occupying up to 91% of gravid proglottis width. Uterus with 10-17 (JNT = numerous) lateral medullar ramified diverticles on each side (Fig. 4) and one or sometimes several ventral apertures as described for *Crepidobothrium* spp (de Chambrier, 1989a, b). Eggs, measured in whole preparations, with oncosphere 11-12 in diameter (JNT = 7.5-11), hooklets 5-6 long; embryophore 13-14 in diameter (JNT = 15-19); outer envelope 60-75 in diameter.

***Ophiotaenia* sp.**

Figs 7-10

Proteocephalus hylae; Prudhoe & Bray, 1982: 33, Figs 8a, b, c.
[Not *Ophiotaenia hylae* Johnston].

Host: *Litoria moorei* (Copland, 1957) (Amphibia : Hylidae).

Locality: Neighbourhood of Perth (Cannington and Darlington), W.A., Australia.

Material studied: 9 whole mount preparations and material in alcohol (from where SEM microphotographs come from) ex *Litoria moorei*, Cannington, Western Australia, 17.04.1966: BMNH 1968.4.19.1-15; 1 whole mount preparation SAM 21402, Darlington, W.A., 12.11.1980.

Site of infestation: Intestine.

DESCRIPTION

Proteocephalidea, Proteocephalidae. Testes, ovary, uterus diverticles in medulla, uterine stem cortical. Strobila acraspedote, anapolytic. Tegument thick and wrinkled in mature proglottides. Presence of numerous small dorso-ventral muscles.

Scolex 260-340 ($n = 4$, $x = 290$) in diameter, suckers 105-130 in diameter (Fig. 9). Apical organ, 50-80 in diameter, covered by small dense spiniform microtriches (Fig. 10). Longitudinal internal musculature dense, formed by 4-5 thick bundles of fibres on both dorsal and ventral sides (Fig. 8).

Ventral and dorsal osmoregulatory canals crossing cirrus pouch at its middle part, situated between vitelline follicles and testes (Fig. 8). Ventral canal, twice the diameter of the dorsal canal, with numerous narrow secondary canals directed externally.

Testes 46-76 in number ($x = 59$, $n = 30$, $CV = 14\%$) in two dorsal field, with tendency to converge anteriorly and posteriorly, in one or two layers dorsally, not reaching laterally to vitelline follicles (Fig. 8), 50-80 in diameter. Testes 14-26 pre-portal, 6-18 postportal and 23-44 aporal in number. Testes degenerated in gravid proglottides.

Genital pores irregularly alternating, opening between 46 and 57 % ($n = 17$, $CV = 6\%$) of proglottis length. Small genital atrium present. Cirrus pouch pyriform, 175-215 long, $PC = 27-33\%$ ($x = 29\%$, $n = 17$, $CV = 4\%$). Cirrus occupying up to 85% of cirrus pouch length. Vagina anterior (54%) or posterior (46%) to cirrus pouch, with a sub-terminal vaginal sphincter (Fig. 8). When anterior, passing ventrally to the cirrus pouch. Mehlis glands 45-65 in diameter. Vas deferens coiled, between base of cirrus pouch and median part of proglottis, often extending beyond body midline in mature and premature proglottides, extending anteriorly.

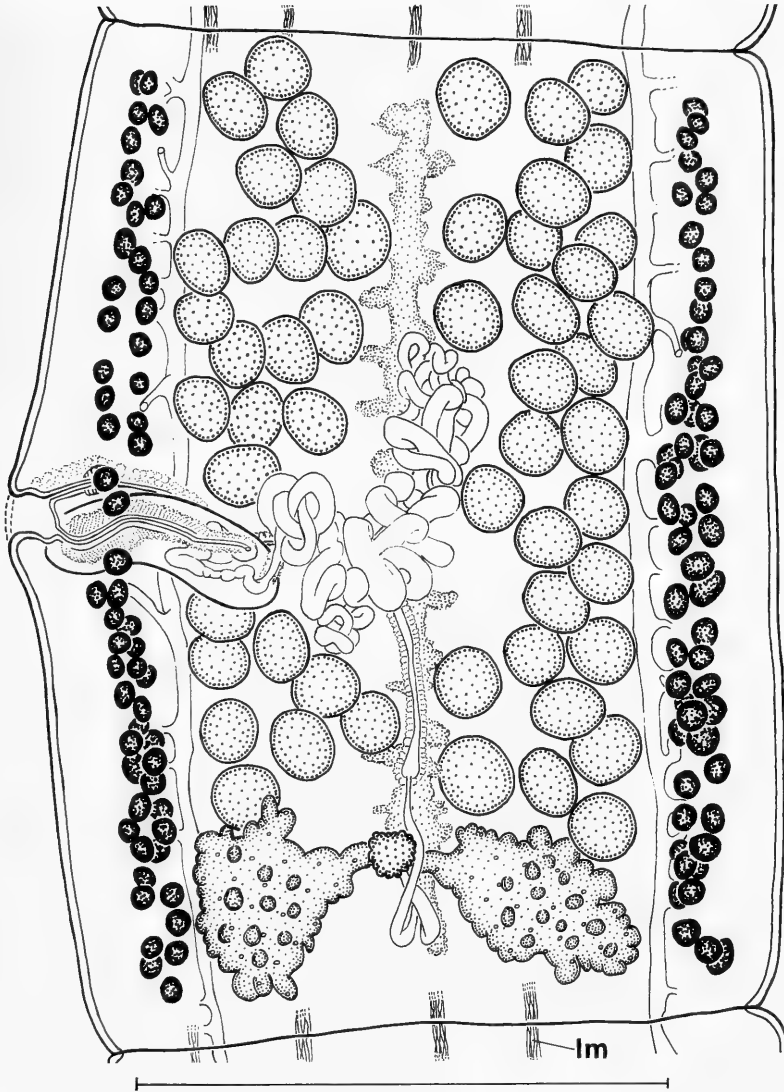
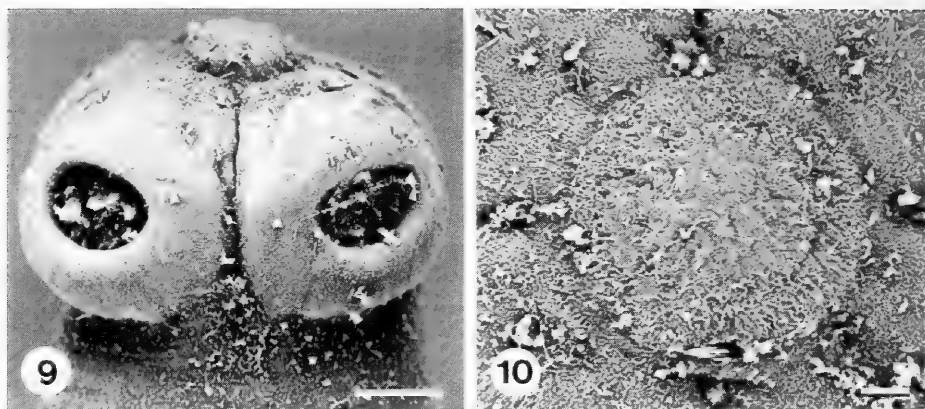


FIG. 8

Ophiotaenia sp. from *Litoria moorei*. 21402 SAM. Mature proglottis, dorsal view. Note the secondary canals ending beneath the tegument. Scale-bar: 500 μ m.

Ovary bilobate, medullary, folliculate, with dorsal outgrowths. OV = 55-63% (\bar{x} = 60%, n = 17, CV = 3%) (Fig. 8). Vitelline follicles, in two lateral bands, occupying porally 87-91% of proglottis length and aporally 86-88% of proglottis length.

Primordium of uterine stem cortical, already present in immature proglottides, with diverticles in medulla. Formation of uterus of type 2 (see de Chambrier *et al.*, 2004).



FIGS 9-10

Ophiotaenia sp., BMNH 1968.4.19.1-15, from *Litoria moorei*. Scanning electron micrographs of the scolex. 9. Dorsoventral view. 10. Apical view, detail of the apical organ. Scale-bars: 9 = 50 μ m; 10 = 10 μ m.

Eggs, measured in distilled water, with oncosphere 12-18 in diameter, hooklets 5-9 long; embryophore 18-23 in diameter; outer envelope up to 55 in diameter (Fig. 7).

REMARKS

This taxon is similar to *Ophiotaenia hylae* on the basis of the following characters: similar apical organ, position of the genital pore, presence of 4-5 dorsal and 4-5 ventral longitudinal internal bundles of musculature. It differs from it by the number of testes (46-76 versus 74-106), by the cirrus pouch length/width of proglottis ratio (27-33% versus 17-19%), and by the ovary width / proglottis width ratio (55-63% versus 68-71%).

Although these observations suggest that it could belong to a new distinct species, the material studied is fragmented and not in suitable conditions for an accurate description. The scolex particularly is badly fixed. In order to confirm that it represents a new species, it would be necessary to collect new material from *Litoria moorei*.

DISCUSSION

Johnston (1912) situated the ovary and the vitelline follicles of *Ophiotaenia hylae* in the cortex. My observations show the ovary to be clearly medullary (see scheme, Fig. 6). As for the vitelline follicles, their position is difficult to assess as there are no clear lateral muscle bundles (Fig. 6). The uterus stem is cortical with further development of diverticles into the medulla (Fig. 6). Contrary to the opinion of Johnston (1912, p. 64), the uterus does not arise as "a thin duct..." but is clearly of the type 2 of uterine development as described by de Chambrier *et al.* (2004). According to Johnston (1912), the vagina is situated anterior and ventral to the cirrus pouch. I observed a position mainly posterior (62%) of the vagina. I also observed a small sub-

terminal vaginal sphincter, secondary canals emerging from the ventral osmoregulatory canal ending under the tegument and the position of vas deferens which extends anteriorly (see Fig. 3).

The structure of the internal longitudinal musculature is also uncommon within the Proteocephalidea. It is composed by 4-5 dorsal and 4-5 ventral powerful isolate bundles of musculature easy to observe in immature and mature proglottides but less so in gravid proglottides. Given the stability of this character, the number of bundle in mature proglottides could be discriminant at the specific level as I already proposed for *Crepidobothrium* species (de Chambrier, 1989b, p. 369).

The apical organ is peculiar because of the presence of small spiniform hooklets covering its surface, retractor-like muscles and network of small canals surrounding it. This morphology shows some similarities with that of the Gangesiinae and looks intermediate between the apical organs found in the *Nomimoscolex piraebea* aggregate (Zehnder *et al.*, 2000) and those in the Gangesiinae (de Chambrier *et al.*, 2003). To my knowledge, no other Proteocephalidea have this kind of apical organ. It would be interesting to analyse the two Australian *Ophiotaenia* species described in the present paper using DNA sequences, and compare them with the taxa cited above in order to see if their respective apical organs could represent a possible evolutionary trend or if this structure is homoplastic.

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Chiave di determinazione dei Chiroterri (Mammalia) della Svizzera attraverso l'osservazione al microscopio ottico della struttura dei peli

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Identification key of bats (Chiroptera) from Switzerland based on hair structure observed through optical microscope. - The identification of mammalian hairs by microscope remains an efficient and well-known technique, but only a few studies concern bats. We studied hair morphology of the 29 species listed from Switzerland and present a dichotomic identification key based on overhair morphology observed by using optical microscopes. This key allows to identify most of the genera and also some typical species. The final purpose of this key is to give the possibility to analyse and to identify quickly the hairs found in guano, taken from their bat roosts.

Key-words: Chiroptera - hairs - optical microscope - identification key - guano - Switzerland.

INTRODUZIONE

L'osservazione al microscopio della morfologia dei peli permette di identificare gran parte dei mammiferi europei (Keller, 1978, 1980; Debrot *et al.*, 1982; Teerink, 1991). In questo contesto, tuttavia, gli studi sui Chiroterri non sono molto progrediti, sia per la mancanza di un interesse pratico, sia perché le conoscenze sul gruppo sono recenti (Benedict, 1957; Debrot *et al.*, 1982; Keller, 1986; Teerink, 1991; Meyer *et al.*, 1997). I Chiroterri presentano una struttura dei peli particolare, che li distingue dagli altri mammiferi per la mancanza della parte midollare interna³, per contro le scaglie esterne della cuticola sono ben sviluppate e variamente strutturate, in special modo nei Microchiroterri (Benedict, 1957; Tupinier, 1973; Keller, 1986). Proprio osservando queste strutture singolari al microscopio ottico o elettronico, diversi autori già in passato avevano ventilato l'idea di classificare i Chiroterri sulla base della morfologia dei peli (Benedict, 1957; Tupinier, 1973; Dulic, 1978; Keller, 1986; Charvet & Keller,

³ Fanno eccezione tre famiglie (Pteropodidae, Rhinopomatidae, Megadermatidae) nelle quali la parte midollare dei peli è presente (Benedict 1957). Essa è invece sempre assente nei Microchiroterri europei.

1989; Meyer *et al.*, 1995), tanto che fù possibile arrivare a identificare diverse specie (Keller, 1986; Tupinier, 1973; Keller & Moeschler, 1988; Dove & Peurach, 2001). Fino ad oggi non era però ancora stata realizzata alcuna chiave di determinazione completa utilizzabile al microscopio ottico.

Nel 1986, Keller elaborò una chiave di determinazione basata sulla struttura dei peli per le specie del genere *Pipistrellus* utilizzabile con l'ausilio del microscopio ottico. Tale strumento ha infatti il pregio di essere di facile uso e i preparati necessari non sono complessi da realizzare come quelli per l'analisi al microscopio elettronico (Charvet & Keller, 1989). Il presente studio vuole essere un seguito e un completamento di quel lavoro, presentando una chiave di determinazione che consideri le specie di Chiroterri presenti in Svizzera e consenta di identificare i vari generi (quando possibile anche le specie) a partire dall'osservazione al microscopio ottico della morfologia dei peli.

APPLICAZIONI PRATICHE DELLA CHIAVE DI DETERMINAZIONE

L'utilità pratica della chiave di determinazione presentata consiste nella possibilità che essa offre di analizzare e determinare i peli contenuti all'interno dello sterco dei pipistrelli (Charvet & Keller, 1989). I Chiroterri dedicano infatti parecchio tempo alla pulizia corporea e così facendo ingeriscono rilevanti quantità dei loro peli, che sono molto resistenti e non subiscono alterazioni durante il processo digestivo (Charvet & Keller, 1989). Diviene quindi possibile determinare gli animali a partire unicamente dallo sterco.

In Svizzera la tutela dei pipistrelli è coordinata da due centri nazionali (CCO, KOF)⁴, cui fanno capo esperti e centri regionali che, per definire l'identità delle specie presenti nei rifugi (edifici, solai, grotte ecc.), effettuano spesso catture di animali. Nel Cantone Ticino il CPT⁵ sta attuando un piano d'inventario che attribuisce ai rifugi una differente importanza in base alle specie presenti. L'esperienza ha mostrato che le catture provocano un notevole disturbo alle colonie e si rivelano solitamente laboriose. La possibilità di determinare il pelo contenuto nello sterco prelevato dai rifugi permette rilevamenti veloci e di vaste proporzioni, consentendo di orientare le azioni di cattura verso i rifugi o le aree di maggior interesse. Con questo metodo è inoltre possibile avere importanti indicazioni anche in assenza di animali, per esempio durante l'inverno o in rifugi abbandonati (presenza passata di specie oggi rare o estinte).

Un altro aspetto utile della chiave di determinazione proposta consiste nella possibilità di esaminare il pelo di individui giovani: è infatti noto che la maggior parte dei criteri utilizzati per l'identificazione degli adulti (p. es. lo sviluppo del cranio, delle membra e dei denti) non è valida per i giovani. La struttura del pelo è invece la stessa sia nei giovani sia negli adulti (Keller & Moeschler, 1988). Neppure tra i sessi sono riscontrabili differenze (Benedict, 1957).

⁴ CCO: Centre de coordination ouest pour l'étude et la protection des Chauves-souris, c/o Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6; KOF: Stiftung zum Schutze unserer Fledermäuse in der Schweiz, c/o Zoo Zürich, CH-8044 Zürich.

⁵ Centro protezione Chiroterri Ticino, CH-6714 Semione.

MATERIALE E METODI

La chiave di determinazione è stata realizzata mediante l'osservazione al microscopio ottico di peli prelevati da animali conservati in alcol o a secco nelle collezioni dei Musei di storia naturale di Ginevra (MHNG), Lugano (MCSN), Coira (BNM), Barcellona (Spagna) e del Museo zoologico dell'università di Zurigo (coll. H. P. Stutz), nonché da animali catturati nel loro ambiente naturale durante altre indagini in corso nel Cantone Ticino (nessun animale è stato disturbato espressamente per la chiave). Sono state esaminate 29 specie caratteristiche della chirotterofauna Svizzera: 27 di queste sono citate in Hausser (1995) più due specie, *Plecotus alpinus* (Kiefer & Veith, 2001) e *Pipistrellus pygmaeus* (Jones & Barratt, 1999), scoperte solo di recente, per un totale complessivo di 115 campioni (vedi "Materiale utilizzato").

La struttura dei peli delle diverse parti del corpo di un pipistrello è la stessa (Meyer *et al.*, 1995). I peli analizzati sono stati prelevati principalmente dal dorso e dall'addome, di norma da individui adulti, anche se, come accennato, i giovani presentano la stessa struttura del pelo (Keller & Moeschler, 1988).

La preparazione dei campioni è stata eseguita col metodo descritto da Keller (1978, 1980, 1986) e Charvet & Keller (1989): i peli vengono puliti in xylol e successivamente fissati su vetrino mediante balsamo del Canada.

In generale su ogni pipistrello sono presenti in ordine sparso diversi tipi di peli: i peli lanosi, dalla struttura più semplice, e i peli primari e secondari, assai più strutturati. Per l'elaborazione della chiave sono stati utilizzati unicamente i peli secondari (come suggerito da Tupinier, 1973 e Keller, 1986). Essi sono composti dalla radice (che comprende il bulbo pilifero), dal fusto, che costituisce la gran parte della lunghezza del pelo (nella chiave esso è suddiviso in base, parte centrale e parte apicale) e infine dalla spatola, tipica appendice a forma di lancia (Fig. 1).

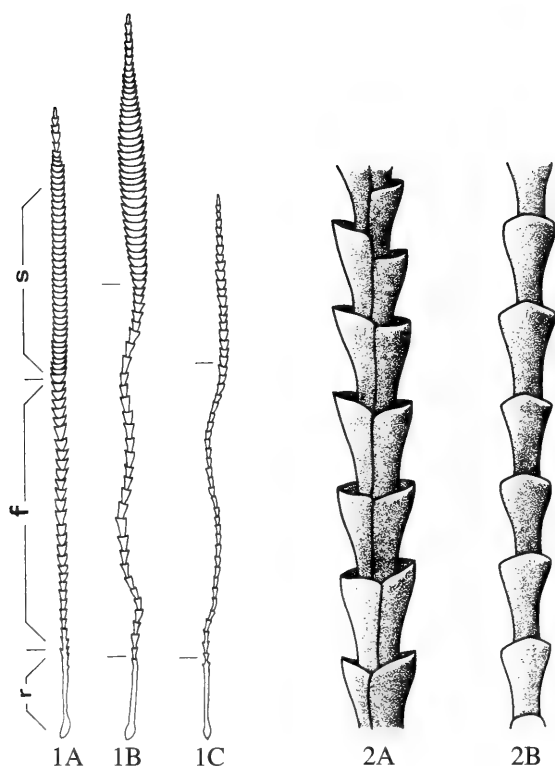
Lo studio al microscopio ottico delle forme, delle dimensioni e delle peculiarità di ciascuna di queste parti del pelo ci ha permesso di confrontare e identificare i vari generi (e talune specie). Particolarmente importante è stata l'osservazione della disposizione, della forma e dell'inclinazione che assumono le scaglie della cuticola (Fig. 2). In Benedict (1957), Tupinier (1973), Charvet & Keller (1989) sono descritti i diversi tipi di forme che esse possono assumere. Ai loro testi facciamo riferimento, quando parliamo di scaglie coronali o imbricate, che possono essere appiattite contro il fusto, divergenti o divaricate. Gli ingrandimenti usati per le osservazioni sono di 200, 400, e 1000 volte.

Al fine di agevolare l'utilizzo pratico della chiave, nelle note a piè di pagina sono integrate alcune informazioni sulle dimensioni dello sterco di talune specie. Infatti vi sono specie che, pur presentando una struttura dei peli assai simile, possono essere agevolmente differenziate sulla base di tali criteri (p. es. *Myotis*).

MATERIALE UTILIZZATO

Barbastella barbastellus (Schreber, 1774): BNM 13812, Andeer, GR; BNM 1602, S, Haldenstein, GR; MHNG 1709.071, Saillon, VS.

Eptesicus nilssoni (Keyserling & Blasius, 1839): BNM 11673, Tinizong, GR; BNM 9866, S, Brusio, GR; MHNG 1804.098 Fully, VS.



FIGS 1-2

1: Morfologia generale dei peli: A, peli primari; B, peli secondari; C, peli lanosi. r, radice; f, fusto; s, spatola. 2: Morfologia delle scaglie della cuticola dei peli secondari: A, viste di profilo; B, viste di fronte.

Eptesicus serotinus (Schreber, 1774): MHNG 722.35, F, Duillier, VD; MCSN VT 3202, M, Lugano, TI; MCSN VT 2614, FS, Cugnasco; MCSN VT 2415, M, Ascona, TI; MCSN VT 2631, M, Cevio.

Hypsugo savii (Bonaparte, 1837): MCSN VT 2662, F, Balerna, TI; MCSN VT 3211, F, Biasca, TI; MCSN VT 2661, F, Taverne, TI; MCSN VT 3209, M, Aquila, TI; MB 82.6812, Barcelona, Spagna.

Miniopterus schreibersi (Natterer in Kuhl, 1819): MHNG 1492.81, M, Kephalovryssion, Argolis, Grecia; MHNG 949.54, M, Otrante, Italia; MCSN VT 17, Lugano, S.Martino, TI.

Myotis bechsteini (Natterer in Kuhl, 1818): MZUZ 5911, Aedermannsdorf; MZUZ 4717, Rechthalten; MZUZ 194, F, Wölflinswil;

Myotis blythi (Tomes, 1857): MCSN VT 2583, F, Gordevio, TI.

Myotis brandti (Eversmann, 1845): MHNG 1805.049, F, Geschinen, VS; MHNG 1684.071, M, Boudry, NE.

Myotis capaccinii (Bonaparte, 1837): MHNG 679.089, Lugano, TI; MHNG 728.052, TI; MHNG 968.001, Massat, Ariège, France.

Myotis daubentoni (Leisler in Kuhl, 1819): MHNG 1684.064, Collonge-Bellerive, GE; MCSN VT 2573, M, Balerna, TI; MCSN VT 2629, M, Locarno, TI; MCSN VT 3217, F, Quinto, TI; MCSN VT 2665, FS, Caslano, TI; MCSN VT 16, Melide, TI. *Ssp. nathalinae*: MHNG 1326.033 (paratype), F, Cabezarrubias, Spagna.

Myotis emarginatus (Geoffroy, 1806): MHNG 1071.014, M, Deluze, Doubs, France; C, F, Brusino, TI; MHNG 722.030, F, Valavran, GE.

Myotis myotis (Borkhausen, 1797): MHNG, M, Crans/Céligny, GE; MCSN V 9, Pavia, Italia; MCSN V 11; MCSN V 10, Pavia, Italia; MCSN V 8, Pavia, Italia;

Myotis mystacinus: MHNG 1684.65, M, Roggwil, BE; C, M, Campo Vallemaggia, TI; MHNG 968.79, M, Champéry, VS.

Myotis nattereri (Kuhl, 1818): MHNG 1714.045, M, La Ferrière, BE; MZUZ 1318, Feldis-Veulden; MHNG 1120.031, M, Vevey, VD.

Nyctalus lasiopterus (Schreber, 1780): MHNG 1010.056, Champéry, VS.

Nyctalus leisleri (Kuhl, 1818): MCSN RC 43; MCSN VT 3210, F, Comano, TI; MCSN VT 3231, F, Someo, TI; MCSN VT 2642, F, Minusio, TI; MCSN VT 2587, Losone, TI.

Nyctalus noctula (Schreber, 1774): MHNG 1702.07, Genthod-Bellevue, GE; BNM 5915, Felsberg.

Pipistrellus kuhli (Natterer in Kuhl, 1819): PZ 434, M, Verona, Italia; MCSN VT 2612, Roveredo, GR; MCSN VT 2616, Chiasso, TI.

Pipistrellus nathusii (Keyserling & Blasius, 1839): MB 82.6808, St.Pere Vilamajor, Spagna; MCSN VT 2478; MCSN VT 2648, Ascona, TI.

Pipistrellus pipistrellus (Schreber, 1774): C, MS, Prugiasco, TI; C, Pura, TI; C, Monte, TI; C, Villaluganese, TI; C, Lavorgo, TI.

Pipistrellus pygmaeus (Leach, 1825): MB 82.6809, M, Barcelona, Spagna; MHNG 1828.017, M, Genève; C, Locarno, Bosco Isolino, TI; MHNG 1807.089, M, Mte Trodos, Cipro; C, Mte Generoso, TI; MHNG 1826.028, Genève; C, TI; C, Locarno, Bosco Isolino, TI; C, TI; C, Locarno, Bosco Isolino, TI.

Plecotus auritus L., 1758: MHNG 1115.12, M, Ibach, SZ; MCSN VT 3214, F, Nante, TI; MCSN VT 20, Induno, TI; MCSN VT 3206, M, TI; C, M, Ambri, TI.

Plecotus alpinus Kiefer & Veith, 2001: MHNG 1325.81, M, Lienz (Austria).

Plecotus sp. (*austriacus* (Fischer, 1829)/*alpinus*): C, M, Campo Vallemaggia, TI; C, M, Crana, TI; C, M, Salorino, TI. (animali catturati nel 2001 e subito rilasciati, la cattura è avvenuta prima della scoperta della nuova specie *P. alpinus*, Kiefer & Veith, 2001).

Rhinolophus euryale (Blasius, 1853): MHNG 925.75, M, Les Baux de Provence, France; MHNG 905.091, M, Fort l'Ecluse, Ain, France; MHNG 905.092, F, Fort l'Ecluse, Ain, France.

Rhinolophus ferrumequinum (Schreber, 1774): MHNG 1255.42, Tourtenay, France; C, Salorino, TI; MCSN VT 15, Carabbia, TI; MHNG 722.063, M, Andermatt, UR; MHNG 890.009, M, Grotte du Poteux, VS; MHNG 976.073, M, Grotta del Tesoro, TI; MHNG 1255.045, M, Tourtenay, Deux-Sèvres, France.

Rhinolophus hipposideros (Bechstein, 1800): MHNG 1255.49, M, Angliers, France; MCSN VT 39; MHNG 722.054, M, Baar, ZG; MHNG 722.055, M, Baar, ZG; MHNG 722.059, F, Satigny, GE; MHNG 903.033, M, Versoix, GE; MHNG 976.060, M, Genève; MHNG 987.013, M, Pissevache, Vernayaz, VS;

Tadarida teniotis Rafinesque, 1814: MHNG 1065.090, M, Champéry, VS; MHNG 946.001, M, Champéry, VS; MHNG 1044.013, M, Champéry, VS.

Vespertilio murinus Linné, 1758: MHNG 852.30, F, GE; MHNG 1120.037, M, Vevey, VD; MHNG 949.13, M, Col de Bretolet, Champéry, VS; MHNG 1755.095, M, Genève.

(MHNG = Museo di storia naturale di Ginevra; MCSN = Museo cantonale di storia naturale di Lugano; MZUZ = Museo zoologico dell'Università di Zurigo, coll. H.P. Stutz; BNM = Museo di storia naturale di Coira; MB = Museo di zoologia di Barcellona (Spagna); PZ = coll. P. Zingg; C = cattura di animali, dati presso CPT; M = maschio; F = femmina; S = subadulto).

RISULTATI

CHIAVE DI DETERMINAZIONE DELLE FAMIGLIE

- 1 Il fusto forma una linea spezzata (Fig. 3A). La radice del pelo può presentare un rigonfiamento (Fig. 4A). Il pelo è poco pigmentato . . . *Rhinolophidae*
- Il fusto non forma una linea spezzata (Fig. 3B, C) 2

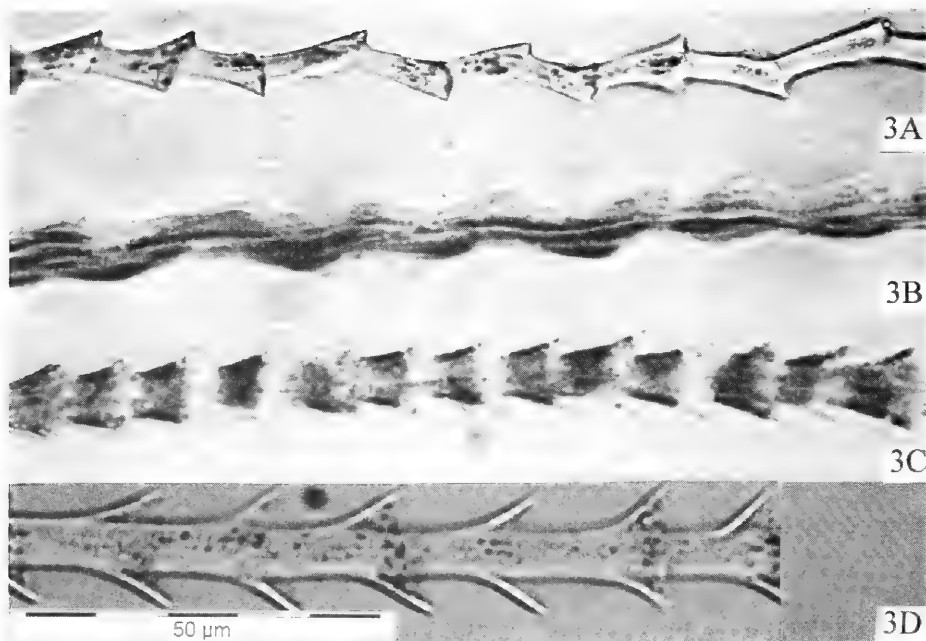


FIG. 3. Fusto. A: *Rhinolophus hipposideros*. B: *Myotis myotis*. C: *Tadarida teniotis*. D: *Tadarida teniotis*, base del fusto.

- 2 Le scaglie del fusto sono asimmetriche e imbricate (Fig. 3B, 7). Possono avere anche un aspetto coronale, tuttavia sono imbricate (Fig. 6A, B, C) Vespertilionidae
- Le scaglie del fusto hanno una struttura simmetrica, coronale e divaricata (Fig. 3C). L'aspetto dei peli è molto caratteristico e uniforme. Alla base del fusto le scaglie formano strutture "a spine" (Fig. 3D) Molossidae: *Tadarida teniotis*

CHIAVE DI DETERMINAZIONE DI GENERI E SPECIE

Rhinolophidae

- 1 Presenza di un rigonfiamento nella radice del pelo (Fig. 4A) 2
- Assenza di un rigonfiamento nella radice del pelo (Fig. 4B) *Rhinolophus euryale*
- 2 Sul fusto alcune scaglie sono coronali e formano ispessimenti (Fig. 4C) *Rhinolophus ferrumequinum*
- Sul fusto le scaglie non formano ispessimenti *Rhinolophus hipposideros*

Vespertilionidae

- 1 Sulla spatola le scaglie sono divergenti (Fig. 5A, B, C) 2
- Sulla spatola le scaglie sono appiattite contro il fusto (fig. 5D, E) 7
- 2 Sulla spatola le scaglie sono molto divergenti e fitte (Fig. 5A) 3
- Sulla spatola le scaglie sono meno divergenti e fitte (Fig. 5B, C) 6

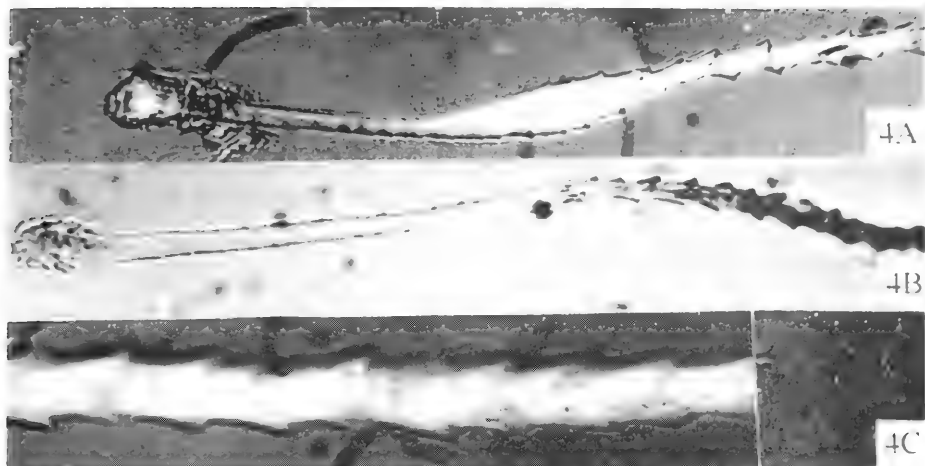


FIG 4. A: *Rhinolophus hipposideros*, radice. B: *Rhinolophus euryale*, radice. C: *Rhinolophus ferrumequinum*, ispessimento del fusto (l'ingrandimento è maggiore rispetto A e B).

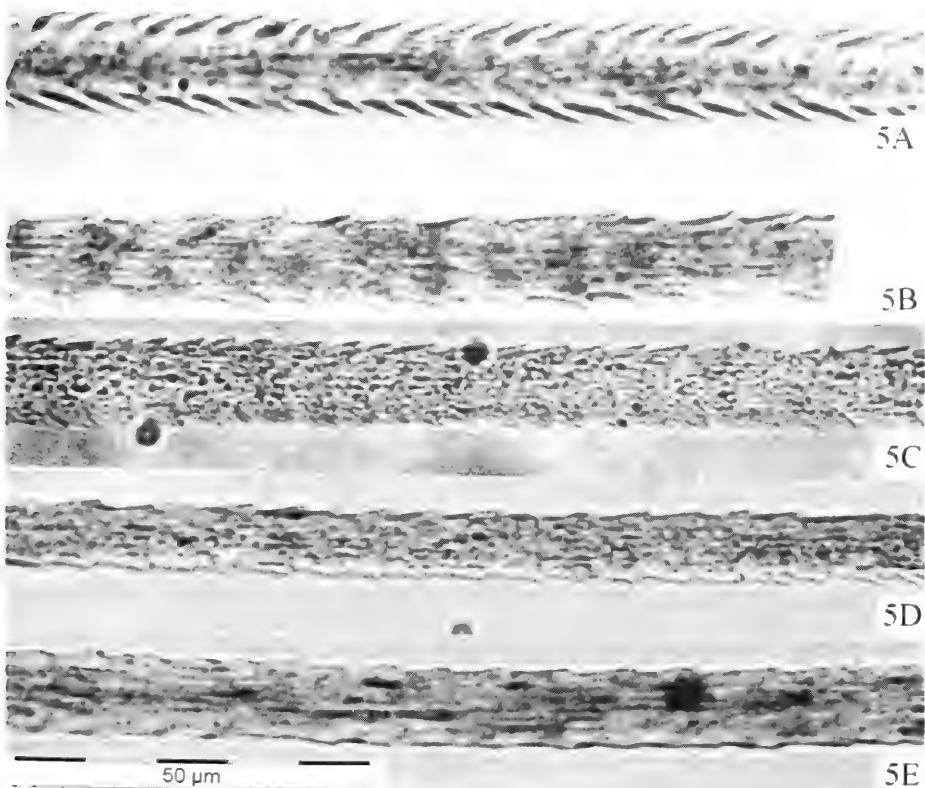


FIG 5. Spatola. A: *Pipistrellus pygmaeus*. B: *Nyctalus lasiopterus*. C: *Vespertilio murinus*. D: *Hypsugo savii*. E: *Myotis myotis*.

- 3 Sulla parte centrale del fusto le scaglie sono caliciformi (Fig. 6A).
I calici possono essere presenti anche sulla base del fusto . . . *Pipistrellus kuhli*⁶
- Sulla base e sulla parte centrale del fusto la maggior parte delle scaglie
non è caliciforme, bensì a forma di imbuto (Fig. 6B, C) 4
- 4 Sulla spatola le scaglie sono divergenti e spaziate (Fig. 6D). Sulla parte
apicale del fusto le scaglie sono talvolta caliciformi 5
- Sulla spatola le scaglie sono divergenti, ma più fitte e appiattite in avanti
(Fig. 6E). Non vi sono spazi tra le scaglie. Di norma mancano le scaglie
caliciformi (difficile) *Pipistrellus nathusii*
- 5 Di norma le scaglie sono meno divergenti (Fig. 6C). Il fusto è più esile
(difficile) *Nyctalus leisleri*⁷
- Di norma le scaglie sono più divergenti (Fig. 6B). Il fusto è più robusto,
con un numero maggiore di strutture caliciformi
. *Pipistrellus pipistrellus*, *P. pygmaeus*⁸
- 6 Sulla parte apicale del fusto le scaglie formano una struttura "a perle"
(cfr. Fig. 7F). Sulla sua base sono invece alternate, robuste e angolose.
La radice è corta e può presentare un rigonfiamento. Pelo marrone
. *Vespertilio murinus*
- Sulla parte apicale del fusto le scaglie non formano una struttura "a per-
le" (Fig. 6F). Il fusto è più esile. La radice è lunga e senza rigonfiamenti.
Pelo marrone chiaro *Nyctalus noctula*, *N. lasiopterus*⁹
- 7 Le scaglie del fusto hanno una struttura molto asimmetrica e formano
una caratteristica linea ondulata marcata e regolare (Fig. 7A)
. *Miniopterus schreibersi*
- L'ondulazione del fusto è poco marcata, irregolare oppure assente (Fig.
7B, C, D, E, F) 8
- 8 Lungo tutto il fusto le scaglie sono appiattite e poco strutturate (Fig. 7E).
L'ondulazione del fusto è pressoché assente 9
- Sulla base e sulla parte centrale del fusto le scaglie sono sempre ben
strutturate, anche se manca ondulazione.
Sulla parte apicale le scaglie possono invece anche essere poco strutturate . . 10
- 9 La radice del pelo è sempre lunga e diritta (Fig. 8A) . Sulla parte apicale
del fusto le scaglie sono simmetriche e poco strutturate (cfr. Fig. 7E)
. *Eptesicus serotinus*¹⁰
- La radice del pelo è più corta e di norma curva o con rigonfiamento (Fig.
8B). Sulla parte apicale del fusto le scaglie formano una struttura "a
perle" (cfr. Fig. 7F) *Barbastella barbastellus*

⁶ Per le specie del genere *Pipistrellus* si rimanda il lettore al lavoro di Keller (1986).

⁷ Lo sterco di *N. leisleri* ($d > 2$ mm) è più grande di quello di *P. pipistrellus/pygmaeus* ($l < 8$ mm, $d < 2$ mm) (l = lunghezza; d = diametro).

⁸ Di norma in *P. pipistrellus* le scaglie della spatola formano un angolo con l'asse principale prossimo ai 45°, mentre in *P. pygmaeus* l'angolo è inferiore ai 45°. Questo criterio è però da considerarsi difficile e incerto.

⁹ Lo sterco di *N. noctula* ($l > 1$ cm; $d \sim 4$ mm) è più grande di quello di *V. murinus* ($d < 4$ mm).

¹⁰ Lo sterco di *E. serotinus* ($l \sim 1$ cm; $d \sim 3$ mm) è più grande di quello di *B. barbastellus*.

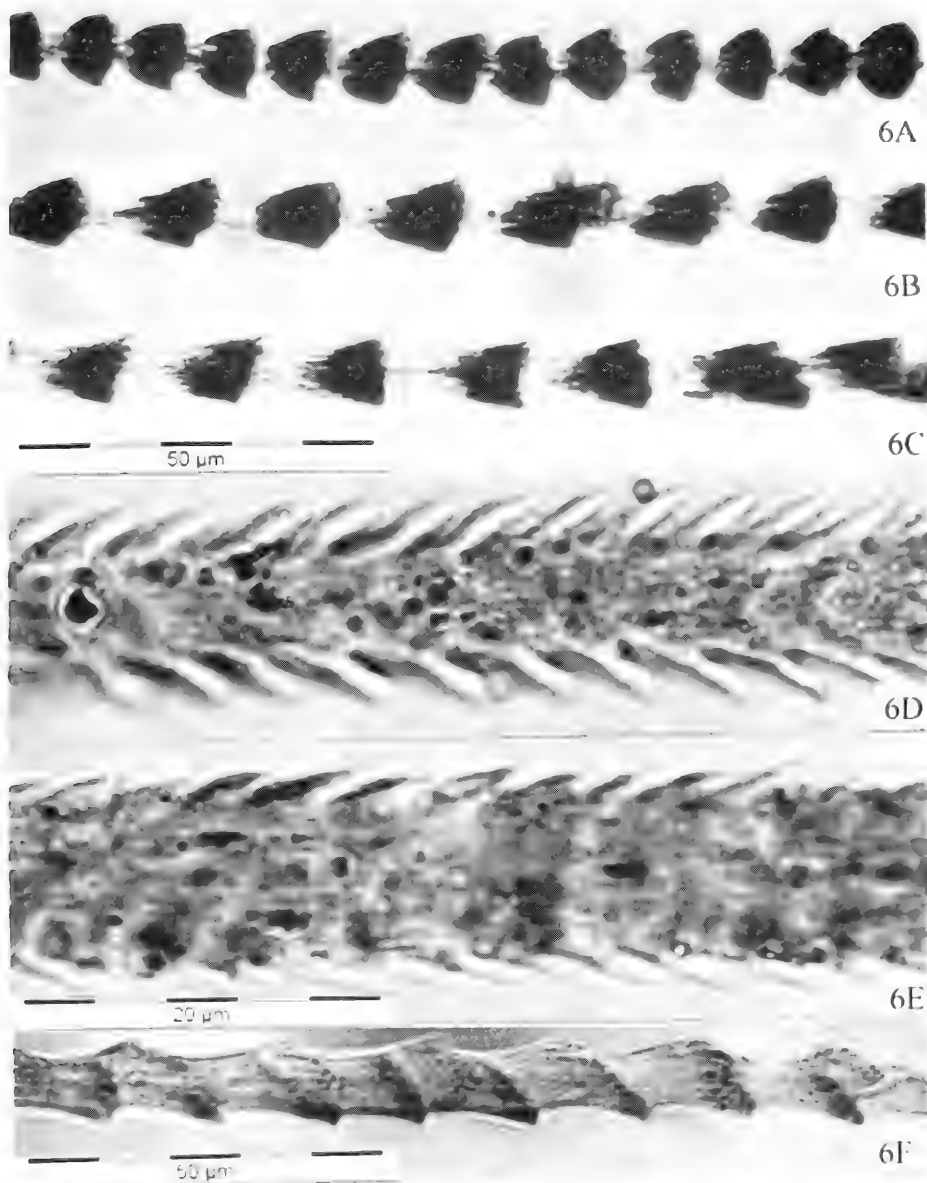


FIG. 6. A: *Pipistrellus kuhli*, parte centrale del fusto. B: *Pipistrellus pygmaeus*, parte centrale del fusto. C: *Nyctalus leisleri*, parte centrale del fusto. D: *Pipistrellus pipistrellus*, spatola. E: *Pipistrellus nathusii*, spatola. F: *Nyctalus noctula*, parte apicale del fusto. (Ingrandimento: D, E, 1000 volte; A, B, C, F, 400 volte).

- 10 Sulla parte apicale del fusto le scaglie formano per un lungo tratto una struttura “a perle” (Fig. 7F). Sulle parti centrale e apicale del fusto l’ondulazione è quasi assente *Hypsugo savii*, *Eptesicus nilssoni*

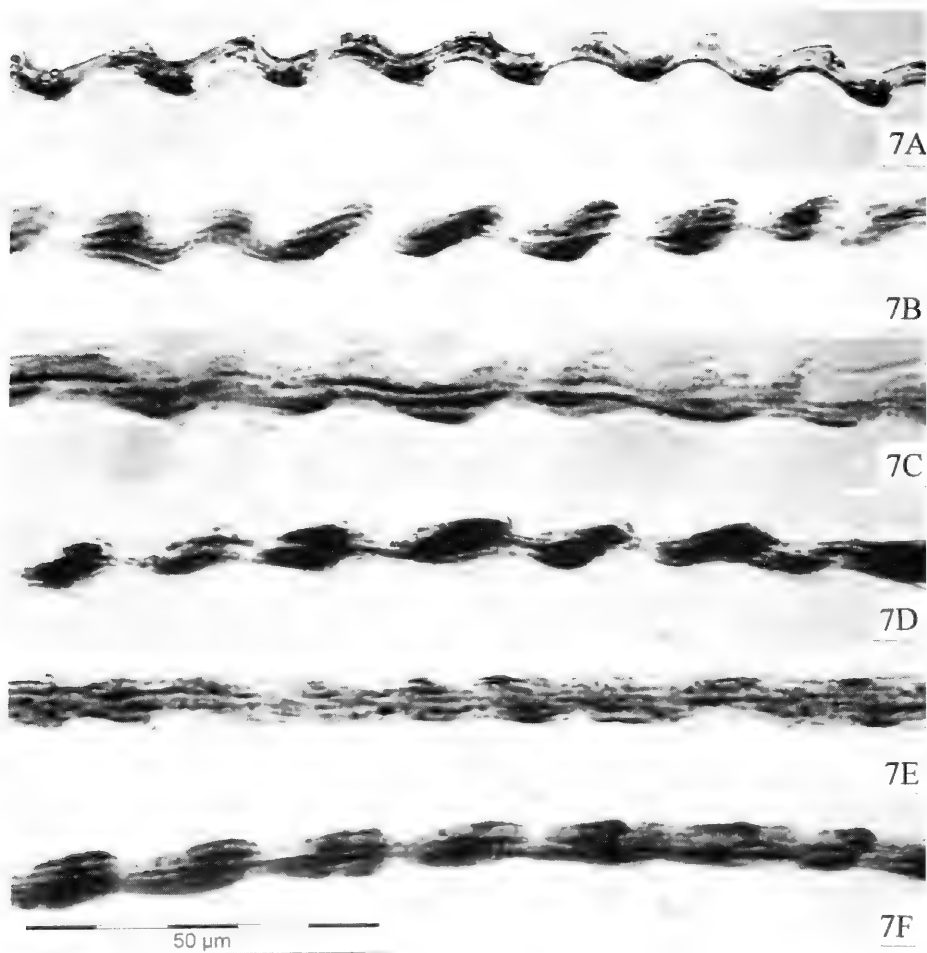


FIG. 7. Fusto A: *Miniopterus schreibersi*. B: *Myotis daubentoni*. C: *Myotis myotis*. D: *Plecotus auritus*. E: *Eptesicus serotinus*. F: *Hypsugo savii*, parte apicale del fusto.

- Sulla parte apicale del fusto la struttura "a perle" è presente solo per un breve tratto oppure è assente. In alcuni tratti il fusto è chiaramente ondulato (fig. 7B, C, D) 11
- 11 Radice corta (< 110 nm) con scaglie corte e subito divergenti (Fig. 8C) *Plecotus* spp.
- Radice lunga (> 110 nm) con scaglie lunghe che divergono gradualmente (fig. 8D, E), oppure con rigonfiamento (Fig. 8F) 12
- 12 La radice presenta sovente un rigonfiamento (Fig. 8F) *Myotis emarginatus*
- La radice è stretta, senza rigonfiamento (Fig. 8D, E) *Myotis* spp.¹¹

¹¹ Lo sterco di *M. myotis* e *M. blythi* si distingue da quello delle altre specie di *Myotis* per le maggiori dimensioni (l > 1 cm; d ~ 4 mm).

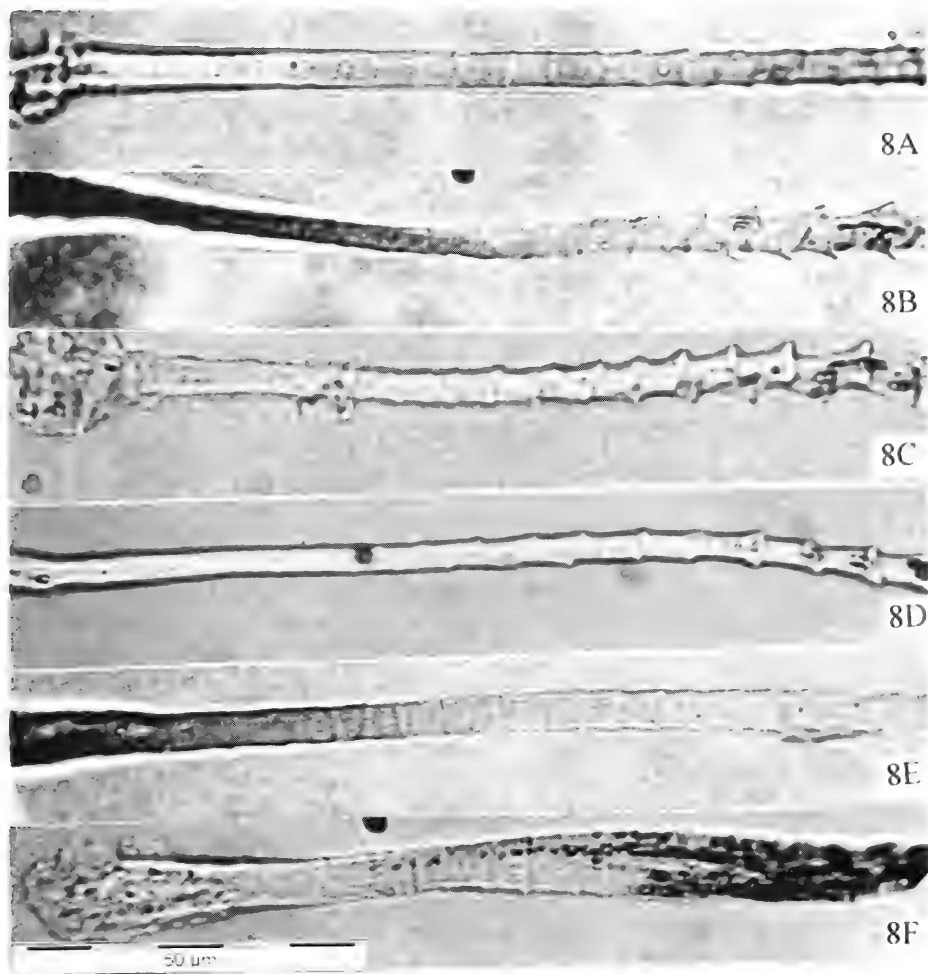


FIG. 8

Radice. A: *Eptesicus serotinus*. B: *Barbastella barbastellus*. C: *Plecotus auritus*. D: *Myotis mystacinus*. E: *Myotis myotis*. F: *Myotis emarginatus*.

DISCUSSIONE

Benedict (1957), che è stato uno dei pionieri in questo campo, aveva già osservato una considerevole variabilità di strutture nei peli dei Microchiroteri. Il nostro lavoro conferma le sue asserzioni, e rivela che molte specie e quasi tutti i generi possiedono una morfologia del pelo tipica. Per esempio *Tadarida teniotis* è l'unica specie a presentare una vera struttura coronale (già citata in Tupinier 1973), mentre *Miniopterus schreibersi* si distingue per una struttura asimmetrica particolare. Il genere *Pipistrellus* ha pure caratteristiche peculiari, tali da permettere l'identificazione delle singole specie (Keller, 1986). Lo stesso vale per i Rinolofidi. Per i *Myotis* la situazione è invece diversa: l'identificazione del genere non è un problema, ma le diverse specie

sono assai simili tra loro e si riesce a separare unicamente *M. emarginatus* (nel caso di peli prelevati dallo sterco, considerato la maggiore taglia, si arriva a separare anche *M. myotis* e *blythi* dalle altre specie).

Pregio della chiave qui presentata è quello di permettere l'identificazione degli animali, indipendentemente dal loro sesso e dalla loro età (Keller & Moeschler, 1988), unicamente sulla base dei peli contenuti nello sterco raccolto nei rifugi, limitando così significativamente il disturbo causato agli animali. Le informazioni fornite da questo tipo di analisi rappresentano un importante aiuto per decidere se e dove proseguire le indagini con le catture per avere ulteriori informazioni sulla colonia (conferma della specie, riproduzione, età, sesso). Nei rifugi abbandonati inoltre si possono ottenere informazioni sulla distribuzione passata di specie in forte regresso o estinte (p. es. Rhinolophidae).

RINGRAZIAMENTI

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Taxonomie der Bernstein-Waldschabe *Ectobius vittiventris* (A. Costa, 1847) (Blattodea: Blattellidae) und ihre Verbreitung in der Schweiz

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Taxonomy of the field-dwelling cockroach *Ectobius vittiventris* (A. Costa, 1847) (Blattodea: Blattellidae) and its distribution in Switzerland. - In this paper we examine the taxonomy of *E. vittiventris* (Ectobiinae) and its distribution and phenology in Switzerland. An illustrated key and a diagnosis are provided to separate the adults from synanthropic cockroaches and from some native *Ectobius* spp. Descriptive notes are included for nymphs and oothecae. We furthermore discuss the taxonomic status of the species and provide information on the type locality and type series, and the same is given for its junior synonyms. In Switzerland *E. vittiventris* is found on both sides of the Alps. In the northern part it is mainly confined to urban areas of the central plateau. On the southern slopes of the Alps it occurs in the cantons Ticino, Valais and Grisons. Our data indicate a rather recent introduction and colonization of urban areas in northern Switzerland, where the species has been recorded mostly after 1985. The altitudinal distribution generally ranges from 260 to about 700 m, with very few records up to 1400 m in the south. Adults are encountered from May to December, with a peak frequency in August. The presence of very small nymphs in summer and of larger nymphs in winter suggests a two-year life-cycle. *E. vittiventris* is frequently encountered inside houses, but apparently it cannot survive under such conditions. A special treatment or control is thus unnecessary. Finally, *E. vittiventris* is recorded for the first time from Germany (Baden-Württemberg).

Key-words: Blattodea - morphology - identification - phenology - pests - *Blattella* - *Blatta* - *Ectobius* - *Periplaneta* - *Supella* - Switzerland.

EINLEITUNG

Mit weltweit nur etwa 4000 Arten (Roth, 1991) sind die Schaben oder Blattodea relativ artenarm. Ihren grössten Artenreichtum weist die ursprüngliche Insektengruppe

in den Tropen und Subtropen auf (Beier, 1967; Roth, 1991). In der Schweiz kommen, je nach Quelle, nur gerade 12-15 Arten vor (Fruhstorfer, 1921; Harz, 1957b; Princis, 1971; Harz & Kaltenbach, 1976). Davon gehören 8-10 Arten zu den frei lebenden Wald- und Kleinschaben der Gattungen *Ectobius* Stephens und *Phyllodromica* Fieber (Blattellidae: Ectobiinae), welche in faunistischer Hinsicht jedoch sehr ungenügend erforscht sind. Wald- und Kleinschaben sind scheue und wenig auffällige Bewohner von Hecken und Waldrändern (Harz, 1957b). Viele Arten leben versteckt im Laub oder unter Steinen. Bei der Eiablage werden die Eier mit einem Drüsensekret umgeben, welches zu einem festen Paket, der sogenannten Oothek, erhärtet (Harz, 1960; Beier, 1967). Die Oothek wird vom Weibchen zuweilen noch mehrere Tage am Abdomenende herumgetragen (Harz, 1960) und schliesslich in die Laubstreu abgelegt (Brown, 1973c) oder vergraben (Harz, 1957a). Für einige Arten wurde ein zweijähriger Entwicklungszyklus festgestellt (Morvan, 1972; Brown, 1973c, 1980; Holuša & Kočárek, 2000). *E. lapponicus* und *E. pallidus* (Olivier) können sich fakultativ parthenogenetisch vermehren (Brown, 1973b). Für die mitteleuropäischen Waldschaben werden *Brachygaster minuta* (Olivier) (Hymenoptera: Evanidae) als Eiparasitoid (Brown, 1973a) sowie *Rhipidius quadriceps* Abeille de Perrin (Coleoptera: Rhipiphoridae) als Nymphalparasitoid (Besuchet, 1956) erwähnt. Wald- und Kleinschaben ernähren sich vor allem von verschiedenen pflanzlichen Stoffen (Harz, 1960), allerdings fehlen gezielte Freilanduntersuchungen zu den einzelnen Arten.

Neben den freilebenden Schaben treten mehrere eingeschleppte, ursprünglich aus südlichen Gebieten stammende Arten regelmässig im Bereich von menschlichen Siedlungen auf. In Mitteleuropa gehören zu diesen synanthropen, kosmopolitischen Arten in erster Linie die Deutsche Schabe *Blattella germanica*, die Braunband-Schabe *Supella longipalpa*, die Küchenschabe *Blatta orientalis*, sowie zwei Arten der Gattung *Periplaneta* (vgl. Weidner, 1993). Durch Massenvermehrung können sie ausserordentlich schädlich werden und stellen als potenzielle Krankheitsüberträger an exponierten Orten (z. B. in Spitälern) ein Gesundheitsrisiko dar (Beier, 1967; Mallis, 1997). Wo sie auftreten, müssen sie daher konsequent bekämpft werden.

Im Laufe der letzten 10-15 Jahre wurden in der Nordschweiz verschiedentlich Meldungen über das Auftreten von Waldschaben in Wohnungen bekannt (Herger, 2000; Landau Lüscher *et al.*, 2003). Ausgehend von den deutsch-schweizerischen Zentren wie Basel, Bern und Zürich wurde man auf die Tiere zunehmend auch in der französischen Schweiz sowie auf dem Land in kleineren Städten aufmerksam. Zunächst wurde angenommen, es handle sich bei diesen ungewöhnlichen Funden um die Lappland-Waldschabe *E. lapponicus* (vgl. Landau *et al.*, 1999), welche in Nordeuropa gelegentlich schon früher in Häusern festgestellt wurde (Harz, 1957b; Weidner, 1972; Abraham, 1979). In einer eingehenden Untersuchung konnten die betreffenden Exemplare jedoch eindeutig als Bernstein-Waldschaben *E. vittiventris* bestimmt werden (Baur, Bohn, Coray, unpubl.). Obwohl sich die Art in Häusern nicht vermehren kann und keinen Schaden anrichtet (Landau Lüscher *et al.*, 2003), ist das Auftreten für die betroffenen Personen dennoch oft unangenehm. Die Bernstein-Waldschabe gleicht bei oberflächlicher Betrachtung nämlich stark der Deutschen Schabe, welche in Wohnungen schädlich wird und deshalb eine Behandlung durch eine Schädlingsbekämpfungsfirma erforderlich macht (Pospischil, 1996).

Die Bernstein-Waldschabe ist eine südeuropäische Art (Ramme, 1951; Harz, 1957b; Harz & Kaltenbach, 1976), die in der Schweiz die Nordgrenze ihrer Ausbreitung erreicht. Bisher war sie nur von der Alpensüdseite, z. B. dem Kanton Tessin, bekannt (Fruhstorfer, 1921, sub *E. neolividus*). Das scheinbar plötzliche Auftreten in der Nordschweiz, noch dazu in Wohnungen, stellte deshalb eine grosse Überraschung dar. In der vorliegenden Arbeit werden nun erstmals Daten zur Taxonomie der Bernstein-Waldschabe und ihrer Verbreitung in der Schweiz ausgewertet. Während mehreren Jahren haben wir alle verfügbaren Angaben zur Verbreitung gesammelt. Von besonderer Bedeutung waren dabei die Erhebungen, welche seit Ende der Achtzigerjahre vom Umwelt- und Gesundheitsschutz Zürich (UGZ) durchgeführt wurden. Ergänzend wurde das Material verschiedener Museen in der Schweiz und im Ausland durchgesehen. Neben der horizontalen sowie vertikalen Verbreitung interessierte uns insbesondere die Phänologie der einzelnen Stadien, um indirekt Hinweise auf den Entwicklungszyklus der Art zu erhalten. Direkte Beobachtungen hierzu fehlten bisher völlig. Ferner haben wir die wichtigsten Merkmale an zahlreichen Museumsbelegen untersucht und in einer Diagnose zusammengestellt. Ein illustrierter Bestimmungs-schlüssel sollte es schliesslich auch dem Nichtspezialisten erlauben, die Bernstein-Waldschabe sicher zu erkennen.

MATERIAL UND METHODEN

Für die vorliegende Studie wurden insgesamt 2000 Datensätze (siehe unten) aus der Schweiz (1984) und Teilen von Deutschland (4) und Italien (12) ausgewertet. Die Untersuchungen zur Morphologie, Verbreitung, Höhenverbreitung und Phänologie basieren ausschliesslich auf Daten aus der Schweiz. Grosse Unterschiede hinsichtlich ihrer Qualität machten eine Unterteilung dieser Daten in zwei Gruppen notwendig, welche in den Analysen jeweils getrennt behandelt wurden. Die eine Gruppe wurde von der Beratungsstelle Schädlingsbekämpfung des Umwelt- und Gesundheitsschutzes Zürich (UGZ) von 1991 bis 1999 und 2001 zusammengetragen und wird als **UGZ-Daten** bezeichnet (1637 Datensätze, vgl. Tab. 1, Appendix 1). Seit 1991 wurden an der Beratungsstelle alle Schädlingsmeldungen systematisch auf EDV erfasst, wobei aber nur die Zahl der Meldungen pro Art und Fundort aufgenommen wurde. Die Anzahl der Individuen, deren Stadien (z. B. Nymphen oder Imagines) etc. wurde dagegen nicht systematisch erhoben. Belege aus diesen Jahren fehlen weitgehend. Seit Beginn der Datenerfassung konnte nun eine Art der Gattung *Ectobius* festgestellt werden, die zwar leicht als Waldschabe zu erkennen war, deren Artzugehörigkeit aber lange Zeit unklar blieb. Erst eine Bestimmung aller Individuen des Jahres 2000 machte deutlich, dass es sich fast ausschliesslich um *E. vittiventris* handelte (Anteil anderer *Ectobius*-Arten < 0,5%). Das gleiche Resultat ergaben die wenigen erhaltenen Belege aus den Jahren 1999 und 2001 (vgl. Appendix 2). Bei der Auswertung der UGZ-Daten konnte deshalb davon ausgegangen werden, dass es sich bei den nicht mehr überprüfbaren Waldschaben der anderen Jahre höchstwahrscheinlich ebenfalls um *E. vittiventris* handelt. Die UGZ-Daten wurden aber wie erwähnt jeweils getrennt analysiert, damit die Grundlage der Resultate überall nachvollziehbar bleibt. Demgegenüber bildete das UGZ-Material des Jahres 2000, welches vollumfänglich im Naturhistorischen Museum Bern aufbewahrt wird, zusammen mit allem anderen Museumsmaterial die Basis der

TABELLE 1: UGZ-Daten 1991-2001. Angegeben ist die Anzahl Datensätze von *Ectobius vittiventris* pro Jahr und Monat (vgl. Material und Methoden; für das Jahr 2000 sind die einzelnen Exemplare in Appendix 2 aufgelistet). "Total" zeigt die Gesamtzahl der Datensätze pro Jahr. "% Ev" entspricht dem Anteil (in %) von *E. vittiventris* an der Gesamtheit aller Tiermeldungen pro Jahr (nur für 1991-2000 berechnet). *Durch eine öffentliche Veranstaltung des UGZ zum Thema "Waldschaben" kamen im Oktober 1999 in Wirklichkeit 100 Meldungen zustande. Diese aussergewöhnlich hohe Zahl stellt aber eindeutig einen Artefakt dar, da die Bevölkerung speziell dazu angeregt wurde, Funde von Waldschaben dem UGZ zu melden. Für die Auswertung (Abb. 22, 24) wurde deshalb der gerundete Oktober-Mittelwert der anderen Jahre (= 16) verwendet.

Jahr	Jan	Feb	Mär	Apr	Mai	Jun	Jul	Aug	Sep	Okt	Nov	Dez	Total	% Ev
1991	0	0	0	0	0	1	5	15	6	3	0	3	33	2.3
1992	0	0	2	0	1	6	35	54	4	6	1	0	109	5.9
1993	0	0	0	0	1	4	8	19	12	12	9	1	66	3.3
1994	0	2	0	0	1	4	56	41	20	20	14	3	161	8.0
1995	0	0	0	0	1	4	37	91	27	22	19	4	205	7.7
1996	2	3	0	0	1	21	61	77	38	25	5	1	234	10.2
1997	0	1	1	0	7	8	32	56	24	15	3	2	149	7.2
1998	0	1	0	2	2	28	103	91	28	14	7	1	277	11.5
1999	4	0	2	1	5	8	18	41	32	*16	34	4	165	6.5
2000	5	4	3	5	12	36	49	75	24	13	13	2	241	10.2
2001	1	1	3	3	9	11	48	101	25	25	9	2	238	—
1991-2001	12	12	11	11	40	131	452	661	240	171	114	23	1878	100

MUS-Daten (347 Datensätze von 600 Exemplaren und 31 Ootheken, vgl. Appendix 2). Für diese Daten wurde jedes Exemplar bestimmt und getrennt nach Geschlecht oder Stadium (Imagines oder Nymphen) erfasst. Die genauen Fundumstände wurden systematisch notiert. Die MUS-Daten bildeten die bevorzugte Grundlage für die meisten unserer Untersuchungen, z. B. zur Morphologie, Verbreitung und Phänologie.

Messungen wurden an Alkoholmaterial, unter einem Stereomikroskop bei 8- (Gesamt-, Körper- und Deckflügelänge), 30- (Pronotumlänge) bzw. 20-facher (Oothek) Vergrößerung, mit Hilfe eines geeichten Okular-Mikrometers (12 mm unterteilt in 120 Einheiten), durchgeführt, anschliessend wurden die Werte in Millimeter umgerechnet. Die betreffenden Exemplare wurden mit einer Etikette mit dem Vermerk "Baur" und einer Seriennummer versehen. Die Gesamtlänge entsprach der Distanz vom Kopf bis zur Spitze der Deckflügel, die Körperlänge derjenigen vom Kopf bis zum Apex der Subgenitalplatte. Der linke Deckflügel wurde in situ von der Basis bis zur Spitze gemessen, die Pronotumlänge entlang der zentralen Längsachse. Die Auswahl der Individuen (vgl. Appendix 2) erfolgte zufällig. In der morphologischen Terminologie folgen wir Roth (1991), einige Begriffe werden zusätzlich in den Abb. 6-8 erläutert. Quantitative Angaben beziehen sich auf die Gesamtheit des MUS-Materials (nur Schweizerdaten) und sind wie folgt definiert: sehr selten < 1%, selten 1-10%, gelegentlich > 10-25%, manchmal > 25-50%, oft > 50-75%, häufig > 75-90%, meist > 90-99%, normalerweise > 99% des vorliegenden Materials. Für die Auswertung der Messreihen wurde SPSS 11.00 (2001) verwendet, für die Erstellung der Verbreitungskarte DMAP, Version 6.5 (1998).

ABKÜRZUNGEN DER KANTONE DER SCHWEIZ

AG	Aargau	OW	Obwalden
BE	Bern	SG	St. Gallen
BL	Basel Land	SH	Schaffhausen
BS	Basel Stadt	SO	Solothurn
GE	Genf	SZ	Schwyz
GR	Graubünden	TI	Tessin
JU	Jura	VD	Waadt
LU	Luzern	VS	Wallis
NE	Neuenburg	ZG	Zug
NW	Nidwalden	ZH	Zürich

ABKÜRZUNGEN DER SAMMLUNGEN

CAN	Coll. Adolf Nadig, in MHNG
CGA	Coll. Georg Artmann, Olten, Schweiz
CKH	Coll. Kurt Harz, in MHNG
ETHZ	Eidgenössische Technische Hochschule, Zürich, Schweiz
MHNG	Muséum d'histoire naturelle, Genève, Schweiz
NHMB	Naturhistorisches Museum, Basel, Schweiz
NMBE	Naturhistorisches Museum, Bern, Schweiz
NML	Natur-Museum, Luzern, Schweiz
UGZ	Beratungsstelle Schädlingsbekämpfung, Umwelt- und Gesundheitsschutz, Zürich, Schweiz, in NMBE
ZMB	Zoologisches Museum, Humboldt Universität, Berlin, Deutschland

RESULTATE

Ectobius vittiventris (A. Costa) - Bernstein-Waldschabe

Blatta vittiventris A. Costa, 1847: 111-112. Syntypen ♂♂ ♀♀, Italien, Campania: Monte Matese, Cusano, coll. ? [Nicht untersucht].

Ectobius neolividus Fruhstorfer, 1921: 78-79. Syntypen ♂♂ ♀♀, Schweiz: Graubünden, Südtessin, coll. CAN, ZMB [1 ♂, 2 ♀ untersucht, s. Appendix 2]. Syn. Ramme (1923: 130).

Ectobius grandis Ramme, 1922: 183-184. Syntypen 10 ♂, 41 ♀, 6 Nymphen, Norditalien: Gardasee, Trient, Val Sugana, Atzwang (nahe Bolzano), coll. ? [Nicht untersucht. Nach Auskunft von Frau Isolde Dorandt, ZMB, befinden sich keine Exemplare, die eindeutig als Syntypen von *E. grandis* zu erkennen wären, in der coll. Ramme; weitere Abklärungen vor Ort und in anderen Sammlungen wären daher wünschenswert]. Syn. Ramme (1923: 130).

Ectobius vitreus Ramme, 1923: 134; Taf. 2, Abb. 8. Syntypen 8 ♂, 5 ♀, Italien, Kroatien, Rumänien, coll. ZMB [1 ♂, 2 ♀ untersucht, s. Appendix 2]. Syn. Ramme (1951: 42).

STATUS

Aufgrund der heutigen Auffassung (z. B. Harz & Kaltenbach, 1976) sind die obigen nominellen Taxa als Synonyme von *E. vittiventris* zu betrachten. Nach Bohn (in litt.) ist es jedoch möglich, dass sich unter diesem Namen mehrere Arten verbergen und die Populationen nördlich vom Apennin (Italien) nicht derselben Art angehören wie die Populationen südlich davon. Die Klärung des genauen Status aller Populationen muss freilich einer umfassenderen Studie vorbehalten bleiben und war nicht das Ziel der

vorliegenden Arbeit. Das im Appendix aufgelistete Material aus der Schweiz, aus Deutschland, Nord- und Mittelitalien gehört unseres Erachtens aber nur einer Art an.

DIAGNOSE

Imagines: Eine der grössten europäischen *Ectobius*-Arten, Länge: Gesamt ♂ 12.4-14.6 mm, ♀ 9.3-11.9 mm, Körper ♂ 10.3-12.3 mm, ♀ 8.4-11.0 mm, Pronotum ♂ 2.2-2.6 mm, ♀ 2.3-2.8 mm, Deckflügel ♂ 10.6-12.1 mm, ♀ 7.8-10.0 mm (vgl. Tab. 2). ♂ von oben betrachtet deutlich schlanker als das ♀. Körper überwiegend ockerfarben (Abb. 15-16). Kopf gelblich bis orangebraun, Gesicht manchmal dunkler. Discus des Pronotums ± einfarbig bernsteinfarben, gelegentlich mit unauffälligen, dunklen Flecken (Abb. 2, 15, 16); Saum heller als Discus, ± durchsichtig. Flügel überragen das Abdomen beim ♂ um ca. 2.0-3.1 mm, beim ♀ um ca. 0.3-2.5 mm; ♂ mit deutlich längeren Deckflügeln als die ♀, Index Deckflügel- / Pronotumlänge ♂ 4.5-4.9, ♀ 3.1-3.8 (vgl. Tab. 2); Farbe der Deckflügel einfarbig glasig gelblich, fein gemustert, aber ohne grössere dunkle Flecken (Abb. 4). Hinterflügel leicht gebräunt, in Ruhelage beim ♀ ungefähr so lang wie die Deckflügel, beim ♂ normalerweise ca. 0.5 mm länger, Analfeld der Hinterflügel mit spiralig aufgerolltem Apikaldreieck. Beine gelblich, Hüften und Schenkel manchmal recht stark gebräunt; Fussglieder meist mit schmalen braunen Ring am Apex. Unterseite der Schenkel nur mit vereinzelt Dornen (Enddornen nicht mitgerechnet): Vorderschenkel 1-3(-4), Mittelschenkel (1-)2-4, Hinterschenkel 1-3(-5), die Bedornung an Vorder- und Hinterschenkel meist nur in der proximalen Hälfte. Abdomenoberseite braun, am Rand und an der Spitze oft aufgehellt (Abb. 7). Drüsengrube queroval, nur an den Rändern mit Haaren besetzt, in der Mitte kahl und höchstens mit schwacher Längserhebung (Abb. 7, 10-12). Zeichnung der Abdomenunterseite hell- bis schwarzbraun; in der distalen Hälfte drei dunkle Längsstreifen erkennbar, diese bei dunklen Exemplaren oft ineinander verschmolzen. Subgenitalplatte des ♂ im Umriss dreieckig, mit nur einem Stylus an der Spitze, höchstens bis zur Mitte von der Supraanalplatte bedeckt (Abb. 7). Cerci schlank, ± gelblich, leicht angedunkelt (Abb. 7). Stylus des ♂ relativ gross, gelblich, oberseits mit honigfarbenem, dichtem Haarstreifen (Abb. 7). Linker Phallomer mit relativ schlankem Haken (Abb. 14).

TABELLE 2: Masse verschiedener Merkmale von *Ectobius vittiventris*.

Merkmal		Minimum	Maximum	Mittelwert	Standardfehler	n
Gesamtlänge (mm)	♂	12.4	14.6	13.59	0.0835	30
	♀	9.3	11.9	10.68	0.0939	30
Körperlänge (mm)	♂	10.3	12.3	11.20	0.0910	30
	♀	8.4	11.0	9.34	0.1156	30
Pronotumlänge (mm)	♂	2.2	2.6	2.44	0.0149	30
	♀	2.3	2.8	2.53	0.0208	30
Deckflügellänge (mm)	♂	10.6	12.1	11.38	0.0675	30
	♀	7.8	10.0	8.85	0.1004	30
Deckflügel / Pronotum	♂	4.5	4.9	4.66	0.0193	30
	♀	3.1	3.8	3.50	0.0246	30

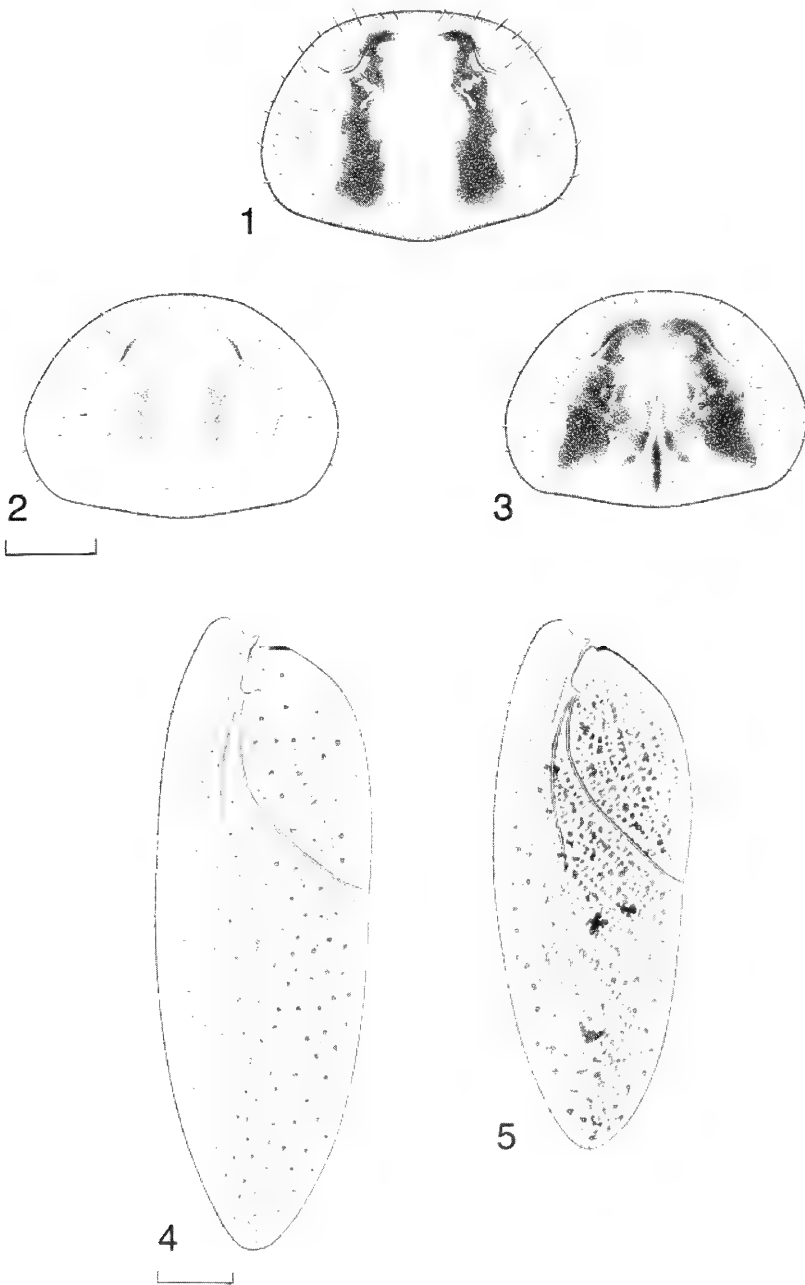


ABB. 1-5

Pronotum ♂: (1) *Blattella germanica* von Bern/BE, (2) *Ectobius vittiventris* von Riehen/BS, (3) *E. lucidus* von Aesch/BL. Linker Deckflügel ♀: (4) *E. vittiventris* von Bottmingen/BL, (5) *E. lapponicus* von Basel/BS. Massstab 1 mm. Zeichnungen A. Coray.

Nymphen: Die einzelnen Nymphenstadien wurden nicht getrennt untersucht. Körperlänge ca. 2.3-7.0 mm. Färbung und Zeichnung ähnlich den Imagines und dadurch leicht von den synanthropen Arten und dunklen *Ectobius*-Arten wie *E. sylvestris* zu unterscheiden: Thorax gelblich, Discus des Pronotums einfarbig bernsteinfarben, rundlich; Pronotum und Mesothorax oft fein gepunktet. Flügelansätze gelblich. Abdomen braun, oft hell gezeichnet. Inwieweit sich die Nymphen von denen weiterer *Ectobius*-Arten unterscheiden, konnte nicht untersucht werden.

Oothek: Länge 2.9-4.9 mm, Breite in der Mitte 2.1-2.7 mm (n=15). Braun bis schwarzbraun. Äussere Form der Oothek (Abb. 9) in Längsrichtung leicht gekrümmt. Trennwände der Eikammern deutlich als feine Querlinien durchscheinend. Oberfläche schwach skulpturiert, auf der ganzen Breite mit zahlreichen, feinsten Längsrippen. Oberkante mit ca. 15-25 Zähnen; Unterseite mit breiter und recht tiefer Längsfurche. Oothek mit 12-23 Eikammern (n=15).

BESTIMMUNGSSCHLÜSSEL

Mit dem folgenden Bestimmungsschlüssel lassen sich die Imagines von synanthropen Schaben sowie von jenen Freilandarten der Gattung *Ectobius*, welche vereinzelt auch in Häusern angetroffen wurden, unterscheiden. Für die Bestimmung der übrigen Wald- und Kleinschaben verweisen wir auf die Arbeiten von Harz (1957b), Harz & Kaltenbach (1976) und Bohn (2000).

- 1 Kleinere Arten, Gesamtlänge ca. 8-15 mm 2
- Grössere Arten, Gesamtlänge ca. 18-40 mm 7
- 2 Deckflügel relativ hell, glasig gelblich bis hellbraun, gelegentlich mit einigen dunklen Flecken (Abb. 4, 5) (Achtung: das dunkle Abdomen kann bei gewissen Arten durchschimmern und einen falschen Eindruck der Deckflügelfarbe erwecken) 3
- Deckflügel mit 1-2 breiten braunen Querbinden, aber nie mit dunklen Flecken *Supella longipalpa* (Fabricius) - Braunband-Schabe
[Discus des Pronotums einfarbig braun, rundlich. Flügel überragen beim ♂ das Abdomenende um 2-3 mm, beim ♀ lassen sie es frei. Hinterflügel in Ruhelage kürzer als Deckflügel, Analfeld der Hinterflügel mit gefaltetem Apikaldreieck. Unterseite der Schenkel stärker bedornt (≥ 8 Dornen), Vorderschenkel über der ganzen Länge mit einer Reihe von 12-15 kurzen Dornen (Enddornen nicht mitgerechnet). Subgenitalplatte des ♂ fast symmetrisch, mit zwei gleich grossen, fingerförmigen Styli.]
- 3 Discus des Pronotums mit variabler Zeichnung aber ohne parallele dunkle Längsstreifen (Abb. 2); falls Längsstreifen angedeutet sind, divergieren diese nach hinten deutlich (Abb. 3) [*Ectobius*-Arten] 4
- Discus des Pronotums mit zwei \pm parallelen, dunklen Längsstreifen (Abb. 1) *Blattella germanica* (Linnaeus) - Deutsche Schabe
[Flügel reichen beim ♂ nicht ganz bis zur Spitze des Abdomens, beim ♀ überragen sie es oft um 3-4 mm. Hinterflügel in Ruhelage ca. 0.5 mm kürzer als Deckflügel, Analfeld der Hinterflügel mit gefaltetem Apikaldreieck. Unterseite der Schenkel stärker bedornt (≥ 8 Dornen), Vorderschenkel über der ganzen Länge mit einer Reihe von 11-14 kurzen Dornen (Enddornen nicht mitgerechnet). Subgenitalplatte des ♂ im Umriss \pm rechteckig, mit zwei unter-

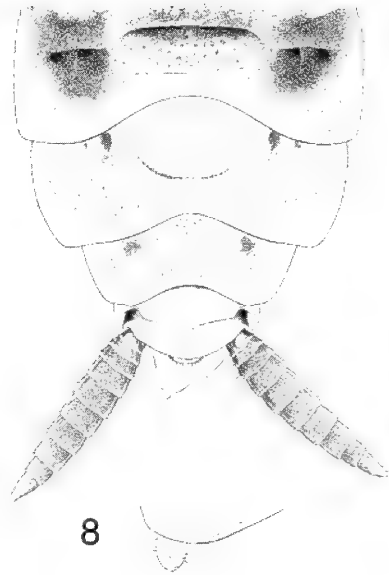
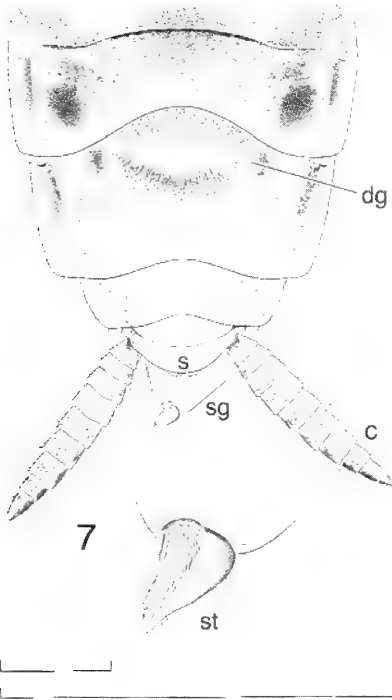
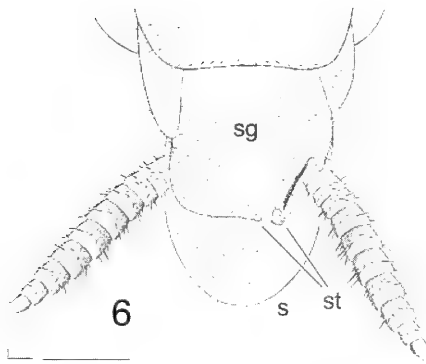


ABB. 6-8

Abdomenende ♂, **ventral**: (6) *Blattella germanica* von Bern/BE. Abdomen ♂, **dorsal**: (7) *Ectobius vittiventris* von Riehen/BS, (8) *E. lucidus* von Aesch/BL. Abkürzungen: c = Cercus, dg = Drüsengrube, s = Supraanalplatte, sg = Subgenitalplatte, st = Stylus. Massstab 1 mm. Zeichnungen A. Coray.

- schiedlich grossen, seitlich gelegenen Styli (Abb. 6); Subgenitalplatte wird bei beiden Geschlechtern von der Supraanalplatte völlig bedeckt und weit überragt (Abb. 6).]
- 4 Discus des Pronotums \pm einfarbig bernsteinfarben, gelegentlich mit unauffälligen, dunklen Flecken (Abb. 2, 15, 16). Deckflügel stellenweise fein gepunktet, aber ohne grössere, dunkle Flecken (Abb. 4); Flügel überragen das Abdomenende in beiden Geschlechtern um 0.3-3.1 mm
 *Ectobius vittiventris* (A. Costa) - Bernstein-Waldschabe
 [Grosse *Ectobius*-Art, Gesamtlänge ♂ 12.4-14.6 mm, ♀ 9.3-11.9 mm. Drüsengrube queroval, nur an den Rändern mit Haaren besetzt, in der Mitte kahl und höchstens mit schwacher Längserhebung, aber ohne Zäpfchen (Abb. 7, 10-12). Stylus des ♂ relativ gross, oberseits mit einem Streifen dicht anliegender Haare (Abb. 7).]
- Discus des Pronotums mit auffälliger, dunkler Zeichnung (Abb. 3) oder ganz dunkel (Abb. 17, 19, 20), falls hell (Abb. 18), dann Deckflügel meist mit deutlichen dunklen Flecken (Abb. 5); Flügel lassen beim ♀ das Abdomenende unbedeckt 5
- 5 Discus des Pronotums ohne betonte Hinterecken, \pm gleichmässig ockerfarben bis dunkelbraun (Abb. 17, 18). Drüsengrube klein, queroval, in der Mitte mit einem dicht mit Haaren besetzten, zweigipfligen Zäpfchen (Abb. 13); Stylus des ♂ gross, ähnlich demjenigen von *E. vittiventris* in Abb. 7 *Ectobius lapponicus* (Linnaeus) - Lappland-Waldschabe
- Discus des Pronotums mit betonten Hinterecken, entweder in der Mitte aufgehellte (Abb. 3) oder gleichmässig braunschwarz bis schwarz (Abb. 19, 20). Drüsengrube gross, nur leicht queroval bis fast halbkreisförmig, in der Mitte zerstreut mit Haaren besetzt, aber ohne Erhebung (Abb. 8); Stylus des ♂ klein (Abb. 8) 6
- 6 Discus des Pronotums in der Mitte \pm aufgehellte (Abb. 3). Deckflügel beim ♀ leicht verkürzt, aber Länge > 6 mm
 *Ectobius lucidus* (Hagenbach) - Hagenbachs Waldschabe
 [Grössere, stärker aufgehellte Art, Länge des Pronotums ♂ 2.4 mm, ♀ 2.6 mm, der Deckflügel ♂ 10.7-11.3 mm, ♀ 6.3-6.5 mm (Durchschnittswerte verschiedener Fundorte aus der Schweiz und Deutschland, nach Bohn, 1989: 323). Drüsengrube leicht queroval (Abb. 8).]
- Discus des Pronotums einfarbig dunkelbraun bis schwarz, meist ohne Aufhellung in der Mitte (Abb. 19, 20); Deckflügel beim ♀ stärker verkürzt, Länge < 6 mm *Ectobius sylvestris* (Poda) - Echte Waldschabe
 [Kleinere, sehr dunkle Art, Länge des Pronotums ♂ 2.0-2.2 mm, ♀ 2.3-2.4 mm, der Deckflügel ♂ 9.7-11.6 mm, ♀ 4.8-5.5 mm (Durchschnittswerte verschiedener Fundorte aus der Schweiz und Deutschland, nach Bohn 1989: 323). Drüsengrube fast halbrund, etwas grösser als bei *E. lucidus* (vgl. Bohn, 1989: 327, Abb. 5). Achtung: gelegentlich haben die ♀♀ ebenfalls ein aufgehelltes Pronotum und können deshalb leicht mit *E. lucidus* verwechselt werden.]
- 7 Flügel verkürzt, beim ♂ das Abdomenende freilassend, beim ♀ schuppenartig, sich nicht berührend. Pronotum einheitlich schwarzbraun
 *Blatta orientalis* Linnaeus - Küchenschabe
- Flügel überragen das Abdomenende in beiden Geschlechtern deutlich. Pronotum braun, \pm aufgehellte 8

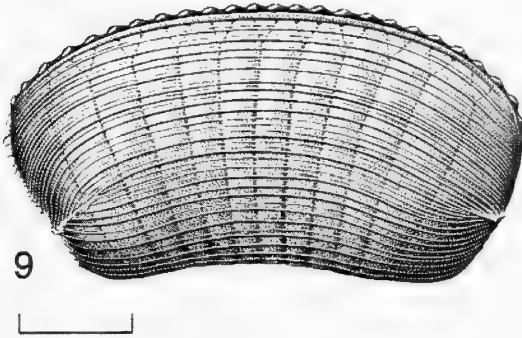


ABB. 9

Oothek: *Ectobius vittiventris* von Bottmingen/BL. Massstab 1 mm. Zeichnung A. Coray.

- 8 Deckflügel einfarbig braun. Dunkle Zeichnung des Pronotums häufig verwaschen, \pm gelblichweiss umrandet
 *Periplaneta americana* (Linnaeus) - Amerikanische Schabe
- Vorderrand der Deckflügel mit elfenbeinfarbenem Streifen, ansonsten braun. Dunkle Zeichnung des Pronotums kontrastreicher und schärfer gegen die gelblichweisse Umrandung begrenzt
 *Periplaneta australasiae* (Fabricius) - Australische Schabe

VERBREITUNG

In der Schweiz ist *E. vittiventris* sowohl auf der Nord- als auch auf der Südseite der Alpen verbreitet (Abb. 21). Im Norden kommt die Art im zentralen und östlichen Mittelland und im Genferseegebiet vor, wobei viele Verbreitungslücken bestehen. Es ist zu beachten, dass die Häufung von Daten in der Umgebung von Bern, Basel, Luzern und besonders Zürich (vgl. Appendizes) allein auf die besonderen Aktivitäten der Autoren und des Ungezieferbestimmungsdienstes des NML zurückzuführen ist! Bemerkenswert ist das fast vollständige Fehlen von älteren Funddaten auf der Alpennordseite. Mit der Ausnahme von einem Exemplar von Küsnacht (ZH) aus dem Jahr 1961 sowie einem undatierten, aber wahrscheinlich in den 50er Jahren gesammelten Männchen von Basel (BS), stammen alle Angaben aus der Zeit nach 1985. Mit Hilfe einer linearen Regression konnte ferner festgestellt werden, dass der Anteil an *E. vittiventris*-Meldungen bei den UGZ-Daten signifikant zunahm ($b = 0.704$, $r^2 = 0.518$, $F = 8.598$, $p < 0.02$, vgl. Abb. 22). In den letzten Jahren war *E. vittiventris* schliesslich die am häufigsten verzeichnete Tierart.

Südlich der Alpen, besonders im Sottoceneri, ist *E. vittiventris* weit verbreitet. Viele Funde gehen hier auf ältere Angaben zurück. Die Feststellung von Fruhstorfer (1921, sub *E. neolividus*), *E. vittiventris* sei "eines der Charaktertiere des südlichen Tessin", hat durchaus noch seine Gültigkeit (Baur, pers. Beob.).

Die Verbreitungskarte (Abb. 21) weist einige markante Lücken auf. So scheint die Art im Jura und auf der Alpennordseite im Wallis und Graubünden weitgehend zu

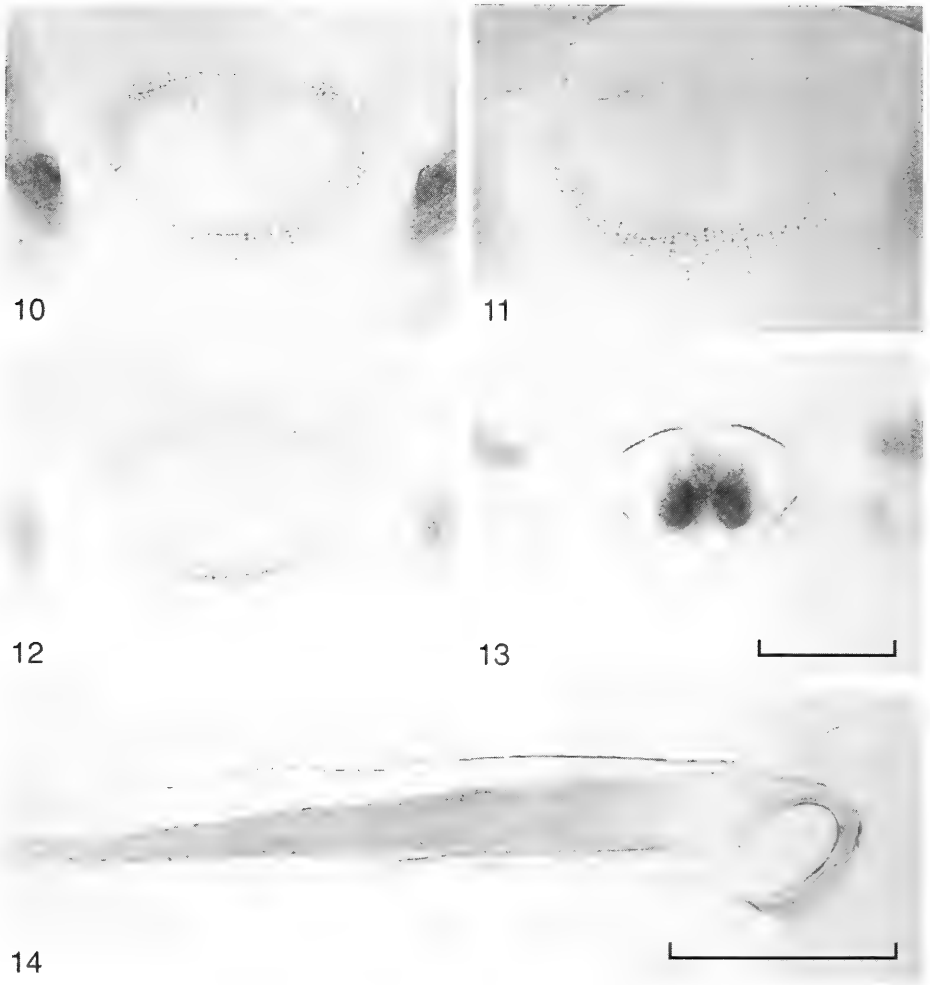


ABB. 10-14

Drüsengrube: (10) *Ectobius vittiventris* von Chavannes-près-Renens/VD, (11) Lancy/VD, (12) Winterthur/ZH, (13) *E. lapponicus* von Eclépens/VD. Linker Phallomer, apikaler Teil: (14) *E. vittiventris* von Chavannes-près-Renens/VD. Massstab 0.5 mm. Fotos H. Baur.

fehlen. Nur zwei Exemplare mit der unspezifischen Angabe "Wallis" befinden sich in CAN bzw. MHNG. Aus dem Oberengadin (GR) lag uns ein einzelnes Männchen von Pontresina aus der Sammlung CAN vor. Dem Exemplar fehlt allerdings das Abdomen, ansonsten stimmt es mit der Diagnose der Art aber einwandfrei überein.

E. vittiventris bevorzugt in der Schweiz die kolline und submontane Höhenstufe bis ca. 600 m ü.M. (Abb. 23). Nur an wenigen Orten steigt die Art nördlich der Alpen auf ca. 1000 m ü.M. (Engelberg, OW). Im Süden ist sie gelegentlich in noch höheren

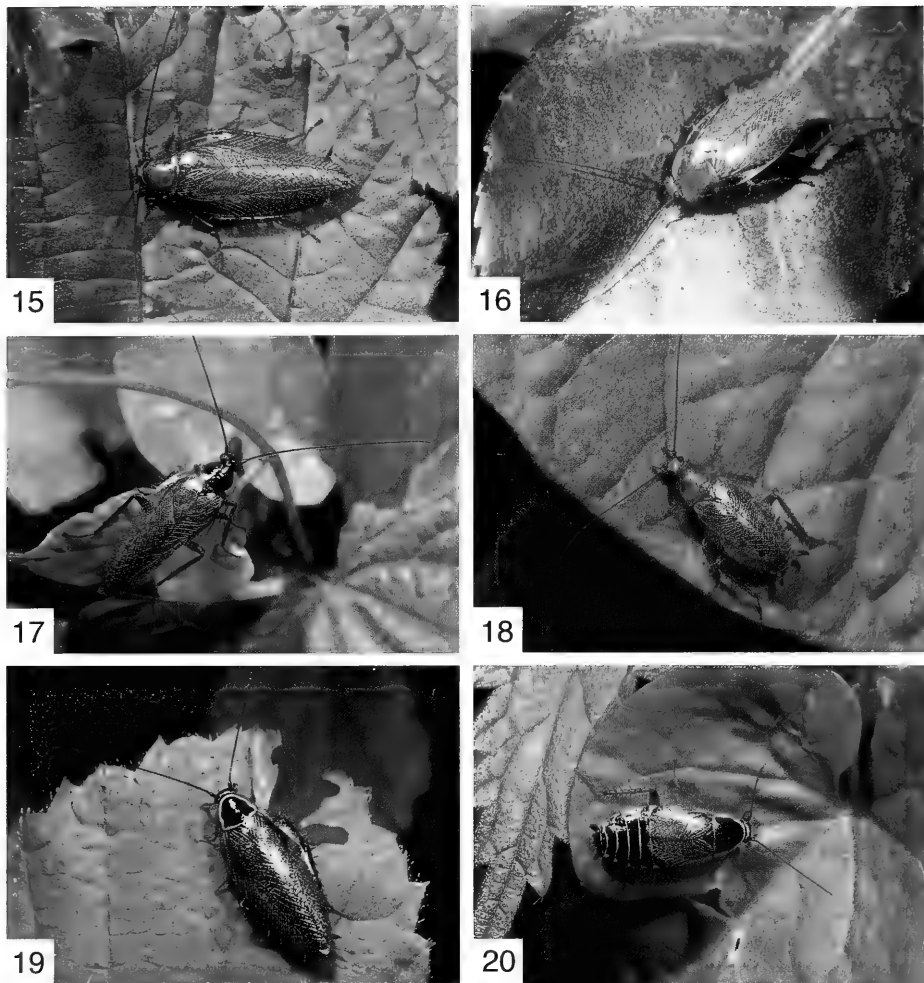


ABB. 15-20

Imagines im natürlichen Lebensraum: (15) *Ectobius vittiventris* ♂ und (16) ♀ von Riehen/BS, (17) *E. lapponicus* ♂ und (18) ♀ von Wehr/Baden-Württemberg, (19) *E. sylvestris* ♂ von Beurnevésin/JU und (20) ♀ von Wehr/Baden-Württemberg. Fotos A. Coray.

Lagen anzutreffen, z. B. wurde sie am Passo Pairolo (TI) auf 1406 m ü.M. von Fruhstorfer gesammelt. Der Einzelfund auf 1800 m ü.M. betrifft das zuvor erwähnte Männchen von Pontresina.

Mehrere Funde von *E. vittiventris* wurden uns aus Baden-Württemberg, Deutschland, mitgeteilt (Appendix 2). Die Art kommt dort entlang des Rheins an mehreren Stellen bis Gottenheim bei Freiburg vor¹.

¹ Das Manuskript war bereits im Druck, als uns 2 Exemplare aus einer Wohnung in Stuttgart, ca. 130 km nordöstlich von Gottenheim, vorgelegt wurden (leg. Oktober 2003, 1 ♀ coll. NMBE, 1 ♀ coll. Matthias Schöller, Berlin).

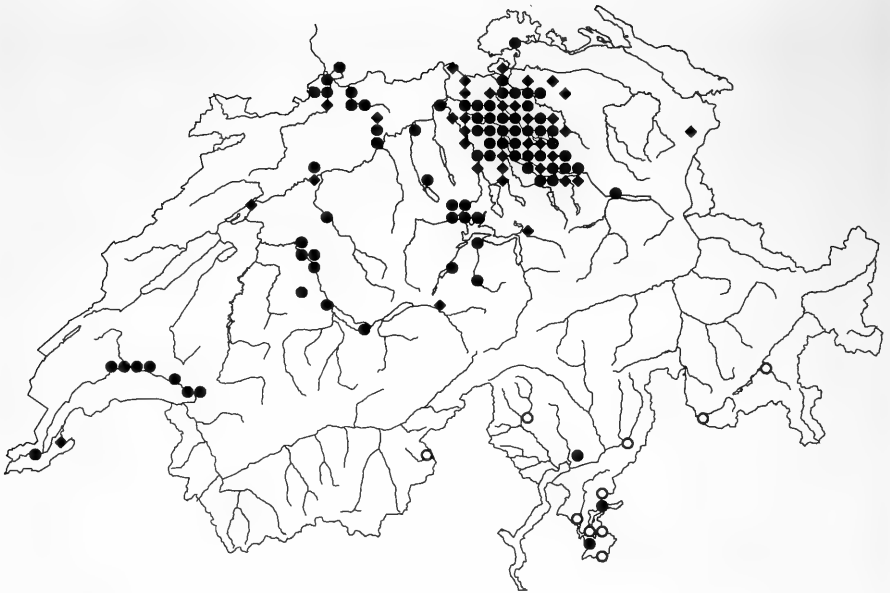


ABB. 21

Verbreitung von *Ectobius vittiventris* in der Schweiz. ○ = Funde vor 1986 (n = 48), ● = Funde nach 1985 (n = 536), ◆ = Funde nur durch UGZ-Daten (n = 1637) belegt (vgl. Material und Methoden).

PHÄNOLOGIE

E. vittiventris kann das ganze Jahr über angetroffen werden. Einen Überblick zum jahreszeitlichen Erscheinen gibt die Abb. 24. Die MUS- und UGZ-Daten zeigen eine recht gute Übereinstimmung. In beiden Fällen wurde die grösste Individuendichte nach einem steilen Anstieg im August registriert; doch bereits im September gingen die Zahlen stark zurück und nahmen bis Dezember kontinuierlich ab. In den Monaten Januar bis April wurden nur vereinzelt Individuen gesammelt. Eine Aufteilung der MUS-Daten nach Geschlecht bzw. Stadium (Abb. 25) zeigte, dass in diesen Monaten ausschliesslich ältere Nymphen (etwa 3.-5. Stadium) gefunden wurden. Die ersten Imagines traten in geringer Anzahl erst ab Ende Mai auf. In den folgenden Monaten nahmen zuerst die Männchen rasch zu und erreichten ihren Höhepunkt im Juli. Das Maximum der Weibchen befand sich rund einen Monat später im August, ab September nahmen aber auch sie schnell wieder ab. Parallel dazu stieg der Anteil gefundener Weibchen mit Oothek von Ende Juni bis in den Oktober. Vereinzelt konnten Imagines schliesslich noch bis in den November und Dezember hinein beobachtet werden.

Die Verteilung der einzelnen Nymphenstadien wurde nicht im Detail untersucht. Wir haben jedoch festgestellt, dass im Winter meist mittlere und grössere Nymphen (ca. 4-7 mm) gefunden wurden. Im Juli konnten gelegentlich noch recht kleine Nymphen gesammelt werden (Bern, Obstberg, 23.7.2000, leg. H. Baur). Einige dieser Exemplare waren deutlich kleiner (2-3 mm, ev. 2. Stadium) als jene vom Winterhalbjahr.

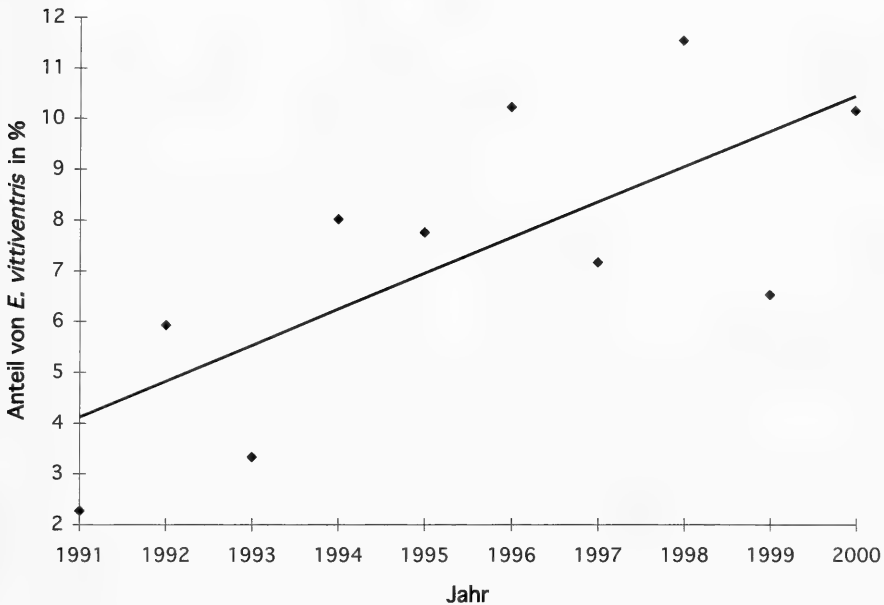


ABB. 22

Lineare Regression des Anteils (in %) von *Ectobius vittiventris* an der Gesamtheit aller durch den UGZ erfassten Tierarten. Die Steigung der Regressionsgerade für die Jahre 1991-2000 ist signifikant ($b = 0.704$, $p < 0.02$; $n_{EV} = 1640$, $n = 21593$).

VERHALTEN

Hierzu können nur Einzelbeobachtungen mitgeteilt werden. *E. vittiventris* ist tagsüber am ehesten in seinen Verstecken anzutreffen, z. B. unter Blumentöpfen, in Rollladenkästen, im Laub oder unter Steinen. Werden die Tiere gestört, suchen sie sofort die nächste Spalte auf. Die Männchen benutzen auf der Flucht oft ihre Flügel, wobei sie im Flug auch an Höhe gewinnen können. Demgegenüber sind die Weibchen höchstens zu einem Sinkflug fähig. In Gebäuden wird *E. vittiventris* oft auch am Tag an ungeschützten Orten angetroffen, während die Art im Freien normalerweise erst in der Dämmerung aktiv wird. Die Tiere krabbeln dann aus ihren Verstecken hervor und klettern auf niederen Zweigen und Laubwerk im Gestrüpp von Waldrändern oder städtischen Grünanlagen umher. Mehrmals konnte beobachtet werden, wie sich mehrere Männchen gegenseitig vertrieben, besonders in Anwesenheit eines Weibchens. Vor der Paarung nähert sich das Männchen dem Weibchen rückwärts mit fast vertikal erhobenen, aber zusammengefalteten Flügeln und bietet so dem Weibchen seine Drüsengrube dar. Bei der endgültigen Kopulationsstellung weisen dann die Köpfe des Pärchens in entgegengesetzte Richtungen. Im Spätsommer und Herbst wurden gelegentlich Weibchen mit Ootheken angetroffen (s. oben). Wo und unter welchen Umständen die Ootheken abgelegt werden, liess sich nicht feststellen. Nymphen unterschiedlicher Grösse wurden regelmässig zusammen mit Imagines auf Blättern und Zweigen, aber auch in Häusern angetroffen.

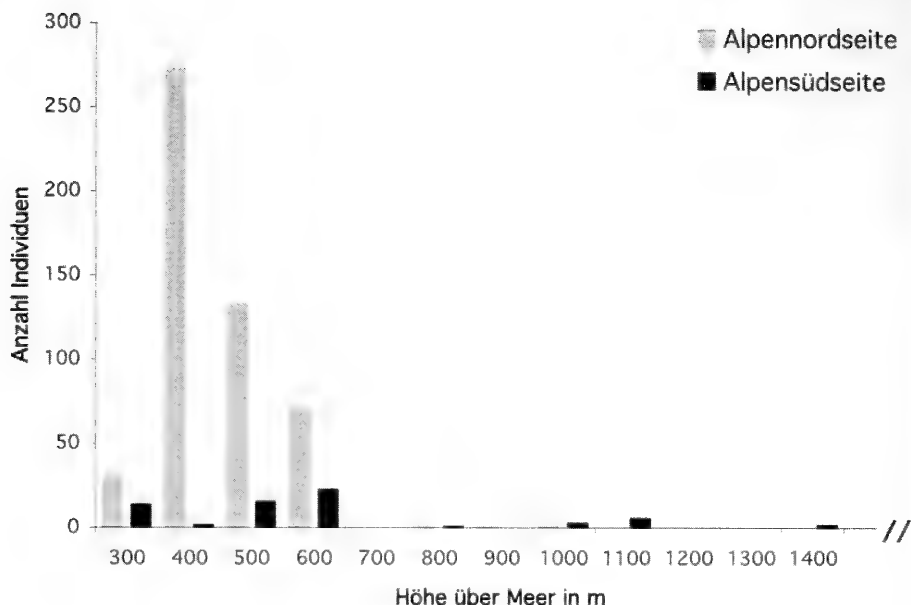


ABB. 23

Höhenverbreitung von *Ectobius vittiventris* in der Schweiz aufgrund der MUS-Daten (Alpennordseite n = 516, Alpensüdseite n = 67). Der Einzelfund auf 1800 m über Meer wurde weggelassen.

FUNDUMSTÄNDE

E. vittiventris konnte im Freien besonders in Hecken und entlang von Waldrändern auf Sträuchern beobachtet werden. Ein Blick auf die MUS-Daten (Appendix 2) zeigt jedoch, dass in der Nordschweiz die allermeisten Funde (> 85%) in oder um Häuser gemacht wurden. Bei den UGZ-Daten dürfte dieser Anteil nahezu 100% betragen. Dies ist nicht weiter verwunderlich, kamen die Mitarbeitenden des UGZ - entsprechend ihrer Tätigkeit - doch nur an Material von solchen Orten heran! Die Daten sind daher ganz offensichtlich mit einem systematischen Fehler behaftet. Da von uns keine gezielten Untersuchungen zum Auftreten dieser Art ausserhalb des Siedlungsbereichs durchgeführt wurden, wird hier auf eine statistische Analyse der Fundumstände verzichtet.

Obwohl *E. vittiventris* oft in Häuser eindringt, haben wir keine Hinweise auf eine mögliche Vermehrung in Gebäuden erhalten. Selbst bei grösseren Vorkommen, wie in Bottmingen, Bruderholz (BL, vgl. Appendix 2), handelte es sich lediglich um Exemplare, die über einen längeren Zeitraum von aussen eindrangen. Nach unseren Beobachtungen kann *E. vittiventris* nicht länger als ein paar Tage in geschlossenen Räumen überleben.

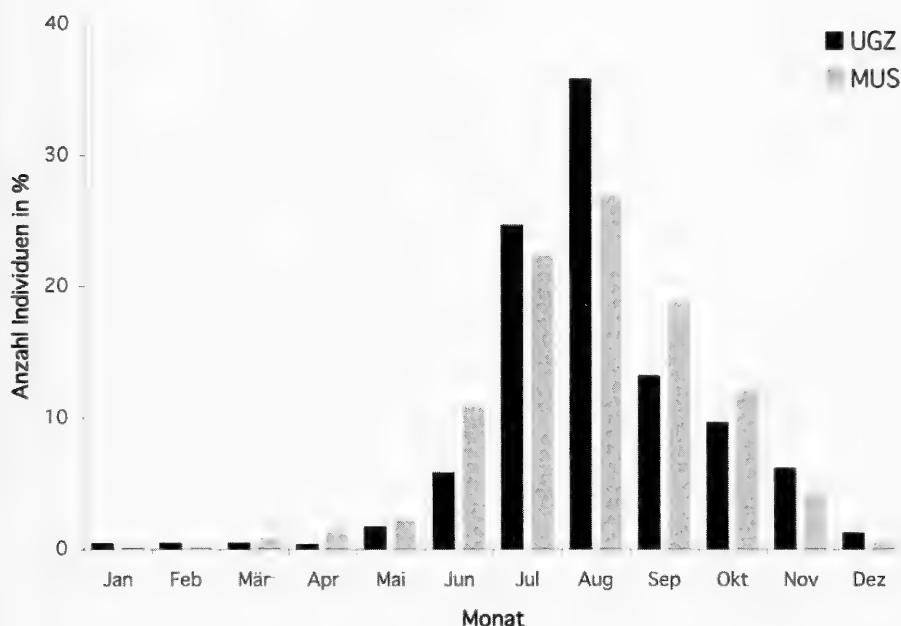


ABB. 24

Phänologie von *Ectobius vittiventris* in der Schweiz nach UGZ- (n = 1637) bzw. MUS-Daten (n = 569). Zum besseren Vergleich erfolgte eine Standardisierung der Anzahl Individuen in %.

DISKUSSION

Eine Analyse der Verbreitungsdaten (vgl. Abb. 21) macht deutlich, dass *Ectobius vittiventris* auf der Alpennordseite fast ausschliesslich nach Mitte der Achtzigerjahre und besonders in städtischen Gebieten gefunden wurde. Dadurch könnte der Eindruck entstehen, dass die Art wahrscheinlich aus dem Süden eingeschleppt wurde und sich danach rasant in den urbanen Regionen ausbreitete. In eine ähnliche Richtung weist die Zunahme des Anteils von *E. vittiventris* an der Gesamtheit aller UGZ-Daten von 1991-2000 (vgl. Tab. 1, Abb. 22). Obwohl eine Verschleppung von *Ectobius*-Arten schon mehrfach dokumentiert wurde (Hoebecke & Nickle, 1981; Chandler, 1985, 1992), kann dieses Szenario durch unsere Daten jedoch nicht eindeutig belegt werden. Das Hauptproblem besteht darin, dass keine älteren Daten zum Vergleich herangezogen werden können. Fruhstorfer (1921) konzentrierte sich in der bisher einzigen faunistischen Bearbeitung der einheimischen *Ectobius*-Arten besonders auf das Tessin, das Wallis und die Bündner Südtäler. Seine Fundortsangaben für die Nordschweiz beruhten zumeist auf unüberprüfbaren Meldungen älterer Autoren. Zudem hatte er viele Arten nachweislich falsch bestimmt (Ramme, 1923, 1951; Zeuner, 1931; Harz, 1957b). Die geringe Beachtung durch Entomologen führte ferner dazu, dass Waldschaben in Sammlungen generell unterrepräsentiert sind. Aufgrund des Fehlens

älterem Meldungen oder Belege kann somit nicht zwingend auf eine rezente Arealerweiterung von *E. vittiventris* geschlossen werden. Es könnte durchaus sein, dass die Art früher sehr wohl vorhanden war, aber verkannt wurde. Hierfür sprechen die beiden Exemplare von Basel (BS) und Küsnacht (ZH) aus den Fünfziger- bzw. Sechzigerjahren (Appendix 2). Demgegenüber lässt insbesondere die Regressionsanalyse der UGZ-Daten (vgl. Abb. 22) den Schluss zu, dass die Grösse der Populationen von *E. vittiventris* in den letzten Jahren stark zugenommen hat. Allerdings könnte dagegen eingewendet werden, dass der Anstieg der Meldungen z. B. auf die zunehmende Beachtung in den Medien zurückzuführen sei. Dieser Effekt hat wahrscheinlich eine gewisse Rolle gespielt, wobei der UGZ nicht zuletzt durch die eigenen Aktivitäten - eine öffentliche Veranstaltung zum Thema Waldschaben im Oktober 1999, Merkblätter im Internet, etc. - mitgeholfen hatte, das öffentliche Interesse an der Schabe zu wecken. Das Ergebnis der Regression allein diesem Umstand zuzuschreiben, scheint uns jedoch nicht gerechtfertigt. Denn dort, wo *E. vittiventris* in den Wohnbereich eindringt, wird dieser Art wegen ihrer Ähnlichkeit mit der Deutschen Schabe *Blattella germanica* schnell einmal Beachtung geschenkt. Deshalb wäre ein Auftreten im gegenwärtigen Ausmass - *E. vittiventris* ist seit 1998 die am häufigsten registrierte Tierart am UGZ - auch in früheren Jahren bemerkt worden und hätte zumindest zu einer weitaus grösseren Zahl von Belegen in Sammlungen führen müssen.

Bei mitteleuropäischen Insekten (Klausnitzer, 1982) und Spinnentieren (Thaler & Knoflach, 1995) sind Zunahmen von Populationen oder gar Arealerweiterungen verschiedentlich dokumentiert worden. Als Beispiel sei die Südliche Eichenschrecke *Meconema meridionale* (A. Costa) (Ensifera: Meconematidae) herausgegriffen, weil hier einige Parallelen zu *E. vittiventris* zu finden sind. Bei den Heuschrecken ist die faunistische Bearbeitung aber vergleichsweise gut (Thorens & Nadig, 1997), weshalb hier weitergehende Schlüsse möglich waren. Noch bis Mitte der Achtzigerjahre war die vorwiegend mediterrane *M. meridionale* nur von wenigen Orten nördlich der Alpen bekannt, in der Schweiz aus dem Tessin, Genferseebecken und unteren Wallis (Nadig, 1981). Im Laufe von wenigen Jahren tauchte die Art dann plötzlich in den meisten Städten in der Nordschweiz auf (Thorens & Nadig, 1997). In Bern, Winterthur und Zürich konnte sie ab Mitte der Neunzigerjahre sogar zusammen mit *E. vittiventris* beobachtet werden (Baur, unpubl.). Da *M. meridionale* in der älteren Literatur für diese Orte nicht erwähnt wird, erscheint eine jüngere Arealerweiterung wahrscheinlich (Thorens & Nadig, 1997). Hinzu kommt, dass die Art und Weise der Ausbreitung durch passive Verschleppung teilweise bekannt ist (Tröger, 1986). Nach Klausnitzer (1982) können sich wärmeliebende Arten wie *M. meridionale* in Städten besonders gut halten, weil diese "Wärmeinseln" durchschnittlich höhere Temperaturen aufweisen als die umliegenden, ländlichen Regionen. Falls *E. vittiventris* sich wirklich rezent nach Norden ausgebreitet hätte, wäre auch diese Art am ehesten in Städten zu erwarten. Unsere Daten lassen freilich auch in dieser Hinsicht keinen eindeutigen Schluss zu, da wir nicht wissen, inwieweit das Vorkommen von *E. vittiventris* tatsächlich auf urbane Regionen beschränkt ist.

Hinsichtlich der Gesamtverbreitung bleibt abzuklären, wie weit *E. vittiventris* ins Walliser Rhonetal vordringen konnte. Wie bereits erwähnt, sind nur zwei Exemplare mit der unspezifischen Bezeichnung "Wallis" bekannt (vgl. Appendix 2). Diese

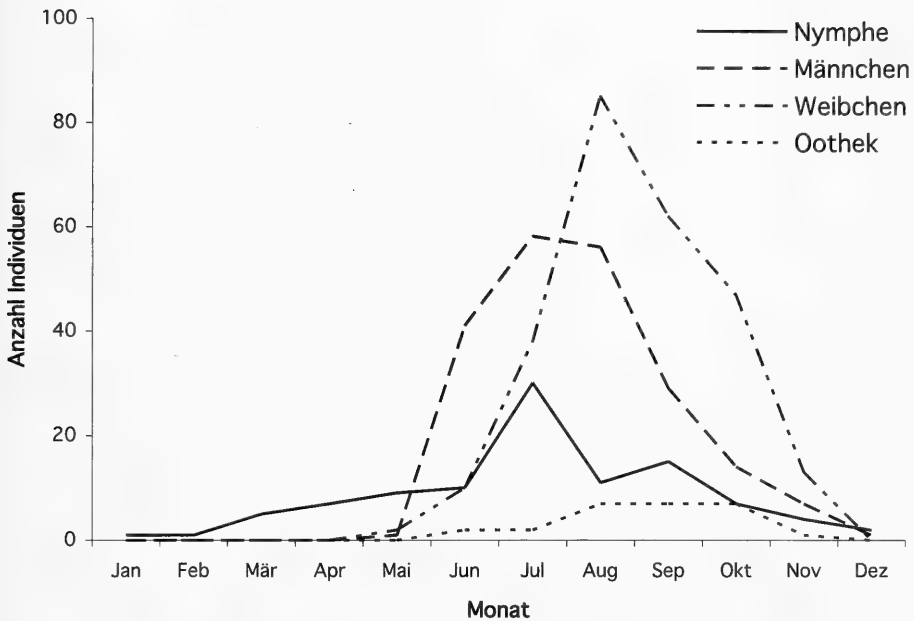


ABB. 25

Phänologie von *Ectobius vittiventris* nach Geschlecht bzw. Stadium (MUS-Daten, n = 596).

könnten z. B. auch von der Alpensüdseite oder dem untersten Wallis an der Grenze zum Kanton Waadt stammen. Demgegenüber ist das Auftauchen von *E. vittiventris* in Baden-Württemberg (vgl. Appendix 2) angesichts der grenznahen Basler Funde nicht überraschend. Die Art wurde für Deutschland aber noch nicht gemeldet (Harz, 1957b; Bohn, 2000).

Die überwiegend kolline bis montane Höhenverbreitung von *E. vittiventris* entspricht derjenigen der meisten anderen *Ectobius*-Arten, einzig *E. sylvestris* ist regelmässig in subalpinen und alpinen Lagen anzutreffen (Harz, 1957b; Baur, Coray, unpubl.). Der Fund eines einzelnen Männchens von *E. vittiventris* in Pontresina auf 1800 m ü.M. fällt somit völlig aus dem Rahmen. Hier wäre eine unbeabsichtigte Verschleppung aus dem nahen Bergell, wo die Art häufig ist, denkbar.

Zur Anzahl der Nymphenstadien und zum Entwicklungszyklus konnten wir keine direkten Beobachtungen machen. Bei einigen *Ectobius*-Arten wurden fünf oder sechs Nymphenstadien festgestellt (Brown, 1973c, 1980), was auch für *E. vittiventris* zutreffen dürfte. Die Phänologie der Imagines, Nymphen und Ootheken (Abb. 25) macht ferner eine zweijährige Entwicklung wahrscheinlich. Das Auffinden von älteren Nymphen im Winter ist ein klarer Hinweis dafür, dass die Postembryonalentwicklung nicht in einem Jahr abgeschlossen werden kann. Der Lebenszyklus könnte daher etwa folgendermassen aussehen: Nach Ablage der Oothek im Sommer und Herbst erfolgt der Schlupf der Nymphen im darauf folgenden Frühjahr. Ein Indiz hierfür sind kleine

Nymphen (höchstens 2. Stadium), welche fast ausschliesslich im Juli gefunden wurden. Der genaue Zeitpunkt des Schlupfes konnte jedoch nicht bestimmt werden, könnte aber ungefähr im Mai oder Juni liegen. Die Nymphen wachsen anschliessend bis zum Herbst langsam heran und überwintern in etwas älteren Stadien. Unsere Funde von grösseren Nymphen in den Wintermonaten machen dies deutlich. Das Alter dieser Nymphen konnten wir nur ungefähr abschätzen, sie befanden sich jedoch mindestens im 2. oder 3. Stadium. Nach dem zweiten Winter reifen die Nymphen schliesslich von Ende Mai bis August zur Imago. Die Imaginalhäutung findet bei den Männchen wahrscheinlich überwiegend im Juli statt, da in diesem Monat die grösste Anzahl von Imagines gefunden wurde (vgl. Abb. 25). Die Weibchen werden durchschnittlich etwa einen Monat später adult.

Für *E. lapponicus*, *E. pallidus* und *E. sylvestris* wurde bereits ein zweijähriger Entwicklungszyklus festgestellt (Morvan, 1972; Brown, 1973c, 1980). Brown (1973c, 1980) zeigte, dass eine Diapause bei niederen Temperaturen für die Entwicklung von *E. pallidus* und *E. lapponicus* obligatorisch ist. Die Überwinterung der Nymphen erfolgte bei *E. pallidus* im 2. bis 5. Stadium (Brown, 1980). Bei *E. lapponicus* konnte Brown (1973c) eine Quieszenz im 2. oder 3. sowie eine fakultative Diapause im 4. Nymphenstadium nachweisen. Erfolgte die Aufzucht bei einer konstanten Temperatur von 20 °C, so konnten sich die Nymphen nicht bis zur Imago entwickeln. In England (Brown, 1973c), Frankreich (Morvan, 1972) und Tschechien (Holuša & Kočárek, 2000) vollzogen die meisten Individuen die Imaginalhäutung bereits im Mai und Juni. *E. lapponicus* ist wie *E. pallidus* (vgl. Morvan, 1972; Brown, 1973c, 1980) also rund ein bis zwei Monate früher adult als *E. vittiventris*. Der Entwicklungszyklus stimmt bei dieser Art somit besser mit demjenigen von *E. sylvestris* in Frankreich überein (Morvan, 1972: 271, Fig. 12).

Zweifellos haben diese Angaben zur Entwicklung von *E. vittiventris* einen etwas vorläufigen Charakter. Sie beruhen aber auf der bestmöglichen Interpretation unserer Daten. Experimentelle Untersuchungen, wie sie von Brown (1973c, 1980) in exemplarischer Weise bei *E. lapponicus* und *E. pallidus* durchgeführt wurden, wären zur Überprüfung der aufgestellten Hypothese sicher zu begrüssen.

Unsere Beobachtungen zum Verhalten von *E. vittiventris* entsprechen ungefähr dem gattungstypischen Muster. Besonders das Paarungsverhalten wird in ähnlicher Weise auch von *E. lapponicus* geschildert (Ramme, 1920; Harz, 1960). Im Unterschied zu den überwiegend tagaktiven *E. lapponicus* und *E. sylvestris* (vgl. Harz, 1957b, 1960; Dreisig, 1971) scheint *E. vittiventris* im Freien vor allem in der Dämmerung und nachts aktiv zu sein. In Häusern ist die Art aber auch tagsüber überall anzutreffen. Damit unterscheidet sie sich in ihrem Verhalten auch von *Blattella germanica*, welche nur nachts aus ihren Verstecken hervorkriecht und sich besonders an feucht-warmen Orten (z. B. beheizte Badezimmer, Küchen) aufhält. Ferner sind beide Geschlechter dieser Art flugunfähig, während die Männchen von *E. vittiventris* über kürzere Strecken fliegen können.

Auch unter Berücksichtigung eines systematischen Fehlers wird deutlich, dass *E. vittiventris* relativ häufig in und um Häuser angetroffen wird (vgl. Appendix 2). Dies führte teilweise zu Verwirrung, da diese Art zumeist mit *Blattella germanica* verwechselt wurde. Wie wir bereits früher festgestellt haben (Landau Lüscher *et al.*, 2003),

muss *E. vittiventris* jedoch nicht bekämpft werden, da die Tiere in Gebäuden offensichtlich nicht mehr als ein paar Tage überleben können. Möglicherweise verhindert auch eine obligatorische Diapause in der Entwicklung der Eier bzw. der Nymphen, wie sie bei anderen *Ectobius*-Arten festgestellt wurde (Brown, 1973c, 1980), eine Fortpflanzung bei Raumtemperatur. Eine Bekämpfung ist daher nicht nur nicht angezeigt, sondern auch nutzlos, da immer wieder neue Exemplare von aussen eindringen.

Das Auftreten von Waldschaben in Gebäuden ist seit längerem bekannt (Weidner, 1972; Abraham, 1979; Jonge, 1984; Chandler, 1985). Ferner beschreibt Mielke (2000) in einer neueren Arbeit einen Massenbefall von *E. lapponicus* in einem Spital in Magdeburg (Deutschland). Allerdings handelte es sich bei all diesen Ereignissen jeweils um Einzelfälle. Im Gegensatz dazu tritt *E. vittiventris* nun schon seit über zehn Jahren regelmässig in Siedlungen in der Schweiz auf. Es ist somit wahrscheinlich, dass die Art sich an diesen Orten bereits etabliert hat.

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APPENDIX 1: UGZ-Daten (vgl. Material und Methoden) der Jahre 1991-1999 und 2001 von *Ectobius vittiventris*. Aufgelistet ist die Anzahl Datensätze (N) pro Ort, sortiert nach Kanton (Kt) und Ort. Die fragliche Meldung von Inden (VS) konnte nicht mehr überprüft werden und wurde in der Auswertung (Tab. 1, Abb. 21, 22, 24) weggelassen.

N	Ort	Kt	N	Ort	Kt	N	Ort	Kt
2	Aarau	AG	4	Birmensdorf	ZH	2	Mönchaltorf	ZH
1	Bremgarten	AG	2	Bonstetten	ZH	4	Nürensdorf	ZH
1	Ennetbaden	AG	1	Brütten	ZH	4	Oberengstringen	ZH
1	Jonen	AG	1	Brüttisellen	ZH	1	Oberhasli	ZH
1	Mellingen	AG	3	Buchs	ZH	4	Oberrieden	ZH
1	Nussbaumen b. Baden	AG	5	Bülach	ZH	2	Obfelden	ZH
2	Rudolfstetten	AG	1	Dielsdorf	ZH	1	Oetwil am See	ZH
1	Spreitenbach	AG	3	Dietikon	ZH	1	Oetwil an der Limmat	ZH
1	Stetten	AG	3	Dietlikon	ZH	4	Opfikon	ZH
1	Suhr	AG	2	Dinhard	ZH	2	Otelfingen	ZH
1	Unterehrendingen	AG	11	Dübendorf	ZH	3	Ottenbach	ZH
1	Wettingen	AG	1	Dürstelen	ZH	3	Regensdorf	ZH
1	Widen	AG	1	Effretikon	ZH	3	Regensdorf, Watt	ZH
1	Würenlos	AG	1	Egg b. Zürich	ZH	1	Richterswil	ZH
1	Zufikon	AG	1	Eglisau	ZH	4	Rümlang	ZH
1	Bern	BE	1	Elgg	ZH	5	Rüschlikon	ZH
1	Ipsach	BE	6	Erlenbach	ZH	1	Russikon	ZH
1	Kilchberg	BL	2	Esslingen	ZH	1	Rüti	ZH
1	Oberwil	BL	1	Fällanden	ZH	6	Schlieren	ZH
1	Reinach	BL	2	Fällanden, Benglen	ZH	1	Schwerzenbach	ZH
3	Collonge-Bellerive	GE	3	Fällanden, Pfaffhausen	ZH	1	Seegräben, Aathal	ZH
1	Lancy, Grand-Lancy	GE	1	Fehraltorf	ZH	1	Stadel	ZH
1	Inwil	LU	2	Gattikon	ZH	2	Stäfa	ZH
2	Meggen	LU	7	Geroldswil	ZH	3	Stäfa, Uerikon	ZH
1	Stans	NW	3	Glattbrugg	ZH	1	Steinmaur	ZH
1	Altstätten	SG	3	Gossau	ZH	8	Thalwil	ZH
1	Amden	SG	2	Greifensee	ZH	4	Uetikon am See	ZH
2	Jona	SG	2	Grüningen	ZH	16	Uitikon-Waldegg	ZH
4	Schaffhausen	SH	1	Grüt bei Wetzikon	ZH	2	Unterengstringen	ZH
1	Dornach	SO	2	Hausen am Albis	ZH	12	Urdorf	ZH
1	Feldbrunnen	SO	3	Herrliberg	ZH	9	Uster	ZH
1	Altendorf	SZ	2	Hinwil	ZH	2	Volketswil	ZH
1	Freienbach, Pfäffikon	SZ	2	Hombrechtikon	ZH	9	Wädenswil	ZH
1	Schwyz	SZ	3	Horgen	ZH	1	Wädenswil, Au	ZH
1	Schwyz, Ibach	SZ	1	Humlikon	ZH	7	Wallisellen	ZH
1	Siebnen bei Wangen	SZ	2	Illnau	ZH	1	Weisslingen	ZH
1	Wollerau	SZ	11	Kilchberg	ZH	3	Wernetshausen	ZH
?	Inden	VS	7	Kloten	ZH	7	Wettswil am Albis	ZH
1	Baar	ZG	4	Küsnacht	ZH	2	Wetzikon	ZH
1	Cham	ZG	5	Langnau am Albis	ZH	1	Winkel bei Bülach	ZH
3	Zug	ZG	2	Männedorf	ZH	1	Winterberg	ZH
11	Adliswil	ZH	1	Maur, Binz	ZH	18	Winterthur	ZH
1	Aeugst am Albis	ZH	4	Maur, Ebmatingen	ZH	11	Zollikon	ZH
6	Affoltern am Albis	ZH	2	Maur, Forch	ZH	10	Zollikon, Zollikerberg	ZH
3	Bassersdorf	ZH	6	Meilen	ZH	7	Zumikon	ZH
1	Bertschikon bei Uster	ZH	9	Meilen, Feldmeilen	ZH	1313	Zürich	ZH

APPENDIX 2: Vollständige Auflistung aller MUS-Daten (vgl. Material und Methoden) von *Ectobius vittiventris*, sortiert nach Land, Kanton, Ort und Datum. Bei Exemplaren bzw. Ootheken, die vermessen wurden, ist die Anzahl fett hervorgehoben. *Die Anzahl der Exemplare von Bottmingen, Bruderholz (BL) wurde aufgrund fehlender Genauigkeit beim Datum in der Auswertung (Resultate, Abb. 23-25) weggelassen. BW = Baden-Württemberg; CH = Schweiz; Coll. = Sammlung (Abkürzungen, siehe Material und Methoden); D = Deutschland; I = Italien; Kt = Kanton bzw. Region (Abkürzungen der Kantone der Schweiz, siehe Material und Methoden); Ld = Land; Mon = Monat; NI = Norditalien; Ny = Nympe; Oo = Oothek; TO = Toskana.

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
1	1	0	0	CH	AG	Aarau	28	6	2000	350	UGZ	Altersheim, Zimmer
0	1	0	0	CH	AG	Aarau	5	10	2000	350	UGZ	
0	1	0	0	CH	AG	Baden	4	8	2000	380	UGZ	
0	0	2	0	CH	AG	Bergdietikon, Kindhausen	29	5	2000	581	UGZ	aussen, unter Blumentöpfen
1	0	0	0	CH	AG	Jonen	8	6	2000	401	UGZ	Haus
0	0	3	0	CH	AG	Umiken	16	3	2000	360	UGZ	Haus
2	0	1	0	CH	AG	Wettingen	4	8	2000	390	UGZ	Haus
0	2	0	1	CH	AG	Wettingen	20	10	2001	390	NMBE	Haus
0	2	1	0	CH	AG	Zurzach				339	UGZ	
0	2	0	2	CH	BE	Bern	30	6	2000	550	UGZ	Kinderkrippe, Sandkasten
0	1	0	0	CH	BE	Bern	7	11	2001	550	NMBE	Haus
0	0	1	0	CH	BE	Bern	16	2	2001	550	NMBE	Wohnung
0	4	0	0	CH	BE	Bern, Breitenrain	10	9	1996	550	NMBE	
0	1	0	0	CH	BE	Bern, Kirchenfeld	21	9	2000	560	NMBE	Haus
2	0	0	0	CH	BE	Bern, Obstberg	21	6	2000	565	NMBE	auf Sträuchern, nachts
0	1	0	0	CH	BE	Bern, Obstberg	3	7	2000	565	NMBE	Umgebung Haus
0	0	20	0	CH	BE	Bern, Obstberg	23	7	2000	565	NMBE	Hecke
0	1	0	0	CH	BE	Bern, Obstberg	4	8	2000	565	NMBE	Wohnung
0	1	0	0	CH	BE	Bern, Obstberg	23	8	2000	565	NMBE	
1	2	0	0	CH	BE	Bern, Obstberg	4	9	2000	565	NMBE	Balkon
0	1	0	0	CH	BE	Bern, Obstberg	29	10	2000	565	NMBE	Wohnung
0	0	4	0	CH	BE	Bern, Obstberg	27	5	2001	565	NMBE	
1	0	0	0	CH	BE	Bern, Obstberg	2	7	2001	565	NMBE	Balkon
1	1	0	1	CH	BE	Bern, Obstberg	8	7	2001	565	NMBE	Haus
0	1	0	0	CH	BE	Bern, Obstberg	25	7	2001	565	NMBE	Balkon
4	1	0	0	CH	BE	Bern, Obstberg	27	7	2001	565	NMBE	Balkon
2	0	1	0	CH	BE	Bern, Obstberg	31	7	2001	565	NMBE	
0	1	0	1	CH	BE	Bern, Obstberg	8	8	2001	565	NMBE	Haus
1	0	0	0	CH	BE	Bern, Obstberg	19	8	2001	565	NMBE	
1	1	0	1	CH	BE	Bern, Obstberg	21	8	2001	565	NMBE	Haus
0	1	0	0	CH	BE	Bern, Obstberg	7	9	2001	565	NMBE	
0	1	0	1	CH	BE	Bern, Obstberg	18	10	2001	565	NMBE	Haus
0	1	0	1	CH	BE	Bern, Obstberg	21	10	2001	565	NMBE	Haus
1	0	0	0	CH	BE	Bern, Obstberg	6	9	2002	565	NMBE	Haus
0	1	0	0	CH	BE	Bolligen	7	8	2001	580	NMBE	Haus
1	2	0	0	CH	BE	Burgdorf			2002	544	NMBE	
0	1	0	0	CH	BE	Burgistein	4	10	1999	751	NMBE	
0	1	0	0	CH	BE	Ittigen	10	8	2000	526	NMBE	Haus
1	0	0	0	CH	BE	Leissigen		7	2000	570	NMBE	7.-8.2000
0	1	0	0	CH	BE	Münsingen	27	5	2001	531	NMBE	Haus
1	0	0	0	CH	BE	Muri	20	6	2000	511	NMBE	Badezimmer
1	0	0	0	CH	BE	Muri	22	6	2000	511	NMBE	Badezimmer
0	1	0	0	CH	BE	Muri, Gümligen	28	6	2000	561	UGZ	Haus
1	0	0	0	CH	BE	Thun	25	7	1992	560	NMBE	Nähe der Aare
1	0	0	0	CH	BE	Worb	26	9	2001	581	NMBE	Garten
1	0	0	0	CH	BE	Worb, Rüfenacht	24	6	1998	590	NMBE	
0	1	0	0	CH	BE	Worb, Rüfenacht	10	9	1999	590	NMBE	
1	0	0	0	CH	BE	Worb, Rüfenacht	25	9	2001	590	NMBE	Garten
1	0	0	0	CH	BE	Worb, Rüfenacht	22	11	2001	590	NMBE	Haus
1	3	80	2	CH	BL	Bottmingen, Bruderholz*			1999	365	NHMB	August-Dezember, am Fenster

APPENDIX 2 (Fortsetzung)

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
1	0	0	0	CH	BL	Füllinsdorf		6	2000	330	NHMB	
0	1	0	0	CH	BL	Liestal		10	2002	450	NHMB	
1	0	0	0	CH	BL	Münchenstein, Teufelsgraben	8	6	2002	270	NHMB	Bachufer
1	0	0	0	CH	BL	Oberwil			1997	305	NHMB	Sommer, Balkon (2. Stock)
1	0	0	0	CH	BL	Oberwil			2002	305	NHMB	Juli–August, Wohnung
0	1	0	0	CH	BL	Sissach		12	1996	370	NHMB	Keller, Totfund
1	0	0	0	CH	BL	Sissach	1	4	1999	370	NHMB	ex Nympha 30.6.1999
1	0	0	0	CH	BS	Basel			1957	270	NHMB	Sammeljahr unsicher!
1	0	0	0	CH	BS	Basel	5	7	2000	270	NMBE	
3	3	0	0	CH	BS	Basel, Bruderholz			1996	310	NHMB	Juli–August
0	1	0	0	CH	BS	Basel, Bruderholz	25	8	1996	310	NHMB	
3	0	0	0	CH	BS	Basel, Bruderholz	17	9	1999	332	NHMB	Haus
0	1	0	0	CH	BS	Basel, Bruderholz		10	1999	332	NHMB	Küche
0	1	0	0	CH	BS	Basel, Bruderholz	1	7	2000	355	NHMB	Haus
0	1	0	1	CH	BS	Basel, Grossbasel west		10	2002	276	NHMB	
1	0	0	0	CH	BS	Basel, Gundeldinger Quartier	17	9	1995	281	NHMB	
1	0	0	0	CH	BS	Basel, Gundeldinger Quartier	7	9	1999	281	NHMB	Wohnung
0	1	0	0	CH	BS	Basel, Kleinbasel	13	9	1999	260	NHMB	Schlafzimmer (2. Stock)
1	0	0	0	CH	BS	Basel, Kleinbasel	24	10	1999	260	NHMB	Wohnung
0	1	0	0	CH	BS	Basel, Kleinbasel, Horburg	5	8	2001	254	NHMB	auf Fruchtstand von <i>Daucus carota</i>
1	0	0	0	CH	BS	Basel, Kleinbasel, Lange Erlen	8	6	2001	260	NHMB	ex Nympha 29.6.2001
1	0	0	0	CH	BS	Basel, Kleinhüningen	23	6	2000	260	NHMB	Badischer Rangierbahnhof
0	1	0	1	CH	BS	Riehen			1999	282	NHMB	Oktober–November
2	0	1	0	CH	BS	Riehen	8	6	2000	286	NHMB	an <i>Buxus sempervirens</i>
0	1	0	0	CH	BS	Riehen	4	7	2000	282	NHMB	
4	2	0	0	CH	BS	Riehen	26	7	2000	285	NHMB	am Fenster (Licht)
0	0	3	0	CH	GE	Lancy	30	8	2000	400	NMBE	Storenkasten von Mietwohnungen
1	0	0	0	CH	GR	Grono		7	1887	332	NMBE	
1	0	0	0	CH	GR	Pontresina			1900	1800	CAN	
1	0	0	0	CH	GR	Roveredo	23	7	1933	292	CAN	23.7.-3.8.1933
1	1	0	0	CH	GR	Soglio	8	1920	1100	CAN		Syntypen <i>E. neolidivus</i> Frühstorfer
0	1	0	0	CH	GR	Soglio	21	7	1929	1100	CKH	
2	0	0	0	CH	GR	Soglio	21	7	1929	1100	CAN	
0	0	1	0	CH	GR	Soglio	21	7	1929	1100	CAN	Bestimmung unsicher
1	0	0	0	CH	LU	Buchrain	24	6	2000	459	NML	auf Balkon
0	1	0	0	CH	LU	Emmen, Emmenbrücke	21	10	1993	436	NML	Wohnung
0	3	0	0	CH	LU	Littau	4	8	2000	511	NML	Balkon, Wohnung
1	0	0	0	CH	LU	Luzern	20	7	1993	430	NML	Wohnung
0	1	0	0	CH	LU	Luzern	8	8	1993	430	NML	Küche, Zimmer
1	0	0	0	CH	LU	Luzern	12	8	1993	430	NML	Wohnung
1	0	0	0	CH	LU	Luzern	19	8	1993	430	NML	Balkon
0	1	0	0	CH	LU	Luzern	21	8	1993	430	NML	Küche, Schlafzimmer
1	1	0	0	CH	LU	Luzern	7	9	1993	430	NML	Balkon, Wohnung
0	1	0	0	CH	LU	Luzern	7	9	1993	430	NML	Wohnung
0	1	0	0	CH	LU	Luzern	10	7	2000	430	NML	Wohnung
1	0	0	0	CH	LU	Luzern	12	7	2000	430	NML	Ausstellungsraum
1	0	0	0	CH	LU	Luzern	2	8	2000	430	NML	Präparatorium
1	1	0	0	CH	LU	Luzern	9	8	2000	430	NML	Wohnung
1	0	0	0	CH	LU	Luzern	28	8	2000	430	NML	Wohnung
1	1	1	0	CH	LU	Meggen	17	10	1999	440	NHMB	
1	0	0	0	CH	LU	Meggen		6	2000	440	NHMB	
2	0	0	0	CH	LU	Rothenburg	16	7	1993	490	NML	Wohnung
2	1	0	0	CH	LU	Sursee	19	7	2000	504	NMBE	Terrasse
1	0	0	0	CH	LU	Sursee	22	8	2000	504	NMBE	Wohnung
0	1	0	0	CH	LU	Sursee	25	7	2000	504	NML	Wohnung
2	0	0	0	CH	NW	Ennetbürgen	27	6	2000	440	NMBE	Balkon
1	1	0	0	CH	OW	Engelberg	5	8	1993	1000	NML	Haus
0	1	0	0	CH	OW	Sarnen		9	1996	470	NMBE	Haus
0	0	1	0	CH	SG	Amden	4	1	2001	908	UGZ	Ferienchalet, Fundjahr 2001
0	0	1	0	CH	SG	Jona	3	11	2000	433	UGZ	Haus
1	0	0	0	CH	SG	Schmerikon	22	6	2000	408	UGZ	
1	3	0	0	CH	SG	Schmerikon	21	7	2000	408	UGZ	Küche und Wohnzimmer
2	2	0	0	CH	SH	Neuhausen	11	2001	440	NMBE	Haus	
0	1	0	0	CH	SH	Schaffhausen	24	8	2000	550	UGZ	
1	0	0	0	CH	SH	Schaffhausen, Alter Emmersberg	5	6	2000	550	NMBE	

APPENDIX 2 (Fortsetzung)

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
0	1	1	0	CH	SO	Riedholz	10	10	2001	530	NMBE	Haus
1	0	0	0	CH	SO	Trimbach, Dürberg, Paradisli	1	7	2001	470	CGA	Waldrand
0	1	0	0	CH	SO	Wangen bei Olten, Haftlet	5	10	2001	505	CGA	Waldrand
0	1	0	0	CH	SZ	Bäch	23	8	2000	411	UGZ	Bank
0	0	1	0	CH	SZ	Freienbach, Pfäffikon	8	5	2000	412	UGZ	Badezimmer
1	1	1	0	CH	SZ	Wollerau	31	8	2000	504	UGZ	Garten und Haus
0	1	0	0	CH	TI	Arzo	20	9	1919	500	ETHZ	Arzo-Meride
1	0	1	0	CH	TI	Arzo, Cava di marmo	25	6	2001	540	NMBE	auf <i>Rubus</i>
0	2	0	0	CH	TI	Arzo-Meride	20	9	1919	500	ZMB	
0	2	0	0	CH	TI	Balerna	9	1919	300	ETHZ	S. Stefano-Balerna	
0	6	0	0	CH	TI	Brusino-Arsizio	12	8	1983	274	MHNG	
0	1	0	0	CH	TI	Capolago	7	9	1919	274	ETHZ	Capolago-Meride
0	1	0	0	CH	TI	Arzo, Monte	4	9	1971	526	ETHZ	
0	1	0	0	CH	TI	Caslaro, Monte	9	9	1971	526	ETHZ	
0	1	0	0	CH	TI	Cevio	7	10	1981	416	MHNG	
0	1	0	0	CH	TI	Chiasso, Pedrinato	7	1919	450	ETHZ		
1	1	0	0	CH	TI	Gandria, Cantine di Gandria	13	7	1989	290	CAN	272-300m
0	1	0	0	CH	TI	Generoso-Crocetta	29	7	1919	1360	ZMB	
0	1	0	0	CH	TI	Gordola	13	10	1987	350	ETHZ	
1	1	0	0	CH	TI	Ligornetto	8	1919	500	CAN		
0	1	0	0	CH	TI	Ligornetto	28	7	1919	500	ETHZ	
1	0	0	0	CH	TI	Ligornetto	28	7	1919	500	ZMB	
0	2	0	0	CH	TI	Ligornetto-Meride	17	9	1919	500	ZMB	
1	2	0	0	CH	TI	Ligornetto-Tremona	8	1919	500	ZMB		
0	1	0	0	CH	TI	Meride	17	9	1919	580	ETHZ	Ligornetto-Meride
0	2	0	0	CH	TI	Meride	27	9	1999	580	NMBE	
3	1	3	0	CH	TI	Meride	25	6	2001	580	NMBE	
0	2	0	0	CH	TI	Meride, Campagna	25	6	2001	620	NMBE	
6	2	0	0	CH	TI	Meride, San Antonio	26	6	2001	570	NMBE	
0	2	0	0	CH	TI	Monte Boglia	7	9	1961	1050	CAN	
0	1	0	0	CH	TI	Monte Generoso	12	9	1960		CKH	genaue Höhe unbekannt!
0	1	0	0	CH	TI	Sonvico, Passo Pairolo	20	6	1919	1406	ZMB	
2	2	0	0	CH	TI	Tremona	8	1919	575	ETHZ	Ligornetto-Tremona	
0	1	0	1	CH	TI	Villa Luganese, Denti della Vecchia	5	9	1919	1000	ZMB	Syntypus <i>E. neolividus</i> Fruhstorfer
1	0	0	0	CH	VD	Chavannes-près-Renens	16	8	1998	403	UGZ	Wohnung
1	2	0	0	CH	VD	Chavannes-près-Renens	20	9	2000	403	UGZ	Aussen, Terrasse
2	0	0	0	CH	VD	Jongny	18	8	2000	550	UGZ	Aussen
0	1	0	0	CH	VD	Lausanne	20	8	1997	500	UGZ	Wohnung
0	1	0	1	CH	VD	Lausanne	8	1998	500	UGZ	Aussen	
0	0	1	0	CH	VD	Lausanne	25	4	2000	500	UGZ	Wohnung
1	1	0	1	CH	VD	Lausanne	10	7	2000	500	UGZ	Wohnung
0	1	0	1	CH	VD	Lausanne	2	8	2000	500	UGZ	Haus und Umgebung
1	0	0	0	CH	VD	Lausanne	22	8	2000	500	UGZ	Haus
0	1	0	0	CH	VD	Lausanne	20	11	2000	500	UGZ	Kindergarten
0	1	0	0	CH	VD	Montreux, Clarens	14	8	1997	400	UGZ	Haus
0	2	0	0	CH	VD	Morges	3	10	2000	375	UGZ	Spital, in Schabenfalle
1	0	0	0	CH	VD	Pully	17	8	2000	425	UGZ	Haus
0	0	1	0	CH	VD	Pully	21	8	2000	425	UGZ	Wohnung
0	1	1	0	CH	VD	Pully	7	9	2000	425	UGZ	Wohnung
0	1	0	0	CH	VD	Pully	14	9	2000	425	UGZ	Wohnung
1	1	0	0	CH	VD	Tour-de-Peilz, La	19	7	1996	400	UGZ	Wohnung
1	0	0	0	CH	VD	Vevey	14	8	1998	380	UGZ	Wohnung
1	0	0	0	CH	VD	Veytaux	10	9	2000	403	UGZ	Hotel
0	1	0	0	CH	VS	Zwischbergen, Gondo	9	9	1957	840	ETHZ	
0	1	0	0	CH	VS				1900		ETHZ	
1	0	0	0	CH	VS						CAN	
1	0	0	0	CH	ZH	Adliswil	12	10	1999	451	UGZ	Wohnung
3	1	0	0	CH	ZH	Adliswil	5	7	2000	451	UGZ	
1	0	0	0	CH	ZH	Affoltern a.A.	14	10	1999	494	UGZ	Wohnung
0	1	0	0	CH	ZH	Affoltern a.A.	5	9	2000	494	UGZ	Haus und Umgebung
1	0	0	0	CH	ZH	Affoltern a.A.	2	10	2000	494	UGZ	Garten und an Fenstern
4	0	0	0	CH	ZH	Bonstetten	7	7	2000	528	UGZ	Haus
0	1	0	1	CH	ZH	Bülach	6	9	2000	420	UGZ	Haus
1	2	1	0	CH	ZH	Bülach				420	UGZ	Wohnung
0	1	0	0	CH	ZH	Dachsen	25	8	2000	393	UGZ	Garten und Wohnung

APPENDIX 2 (Fortsetzung)

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
1	0	0	0	CH	ZH	Dällikon	3	7	2000	438	UGZ	Wohnung
1	0	0	0	CH	ZH	Dietlikon	29	6	2000	444	UGZ	Wohnung und Gartensitzplatz
1	0	0	0	CH	ZH	Dietlikon	29	6	2000	444	UGZ	Restaurant
1	0	0	0	CH	ZH	Dübendorf	5	7	2000	440	UGZ	Attikawohnung
1	1	0	0	CH	ZH	Dübendorf	5	7	2000	440	UGZ	Wohnung
2	1	0	0	CH	ZH	Dübendorf	6	7	2000	440	UGZ	Schlafzimmer
0	1	0	0	CH	ZH	Dübendorf	6	7	2000	440	UGZ	Schlafzimmer
0	1	0	1	CH	ZH	Dürnten	31	8	2000	510	UGZ	
0	1	0	0	CH	ZH	Egg	2	11	1999	540	UGZ	Wohnung
1	0	0	0	CH	ZH	Embrach	21	6	2000	440	UGZ	Haus
1	0	0	0	CH	ZH	Erlenbach ZH	30	6	2000	422	UGZ	Wohnung
0	2	0	0	CH	ZH	Fällanden, Benglen	15	8	2000	600	UGZ	Balkon und Wohnung
0	1	0	1	CH	ZH	Fällanden, Pfaffhausen	15	10	1999	600	UGZ	Haus
0	2	0	0	CH	ZH	Geroldswil	11	7	2000	420	UGZ	Kath. Pfarramt
0	1	0	0	CH	ZH	Geroldswil	13	7	2000	420	UGZ	Haus
2	0	0	0	CH	ZH	Glattfelden	18	8	2000	410	UGZ	Wohnung
0	1	0	0	CH	ZH	Greifensee	19	10	1999	440	UGZ	Haus
0	0	1	0	CH	ZH	Hinwil, Wernetshausen	7	12	1999	800	UGZ	Haus
0	1	0	0	CH	ZH	Hombrechtikon	7	7	2000	500	UGZ	Haus
0	0	3	0	CH	ZH	Horgen	12	4	2000	410	UGZ	Aussen, unter Blumentöpfen
0	1	4	0	CH	ZH	Illnau	6	7	2000	510	UGZ	Wohnung
0	1	0	0	CH	ZH	Illnau, Brunnacher, Ottikon	12	7	2000	600	UGZ	Haus
0	1	0	0	CH	ZH	Küsnacht	17	10	1961	410	ETHZ	Haus
1	0	0	0	CH	ZH	Küsnacht	20	12	2000	410	UGZ	Haus
1	0	0	0	CH	ZH	Maur, Ebmatingen	27	7	2000	610	UGZ	Wohnung
0	0	1	0	CH	ZH	Meilen, Feldmeilen	6	8	2000	480	UGZ	Wohnung
0	0	1	0	CH	ZH	Meilen, Rossbachtobel	19	3	2000	470	UGZ	Balkonkistchen
0	1	1	0	CH	ZH	Neftenbach	19	9	2000	420	UGZ	Haus
0	1	0	1	CH	ZH	Nürensdorf	22	10	1999	505	UGZ	Haus
0	1	0	0	CH	ZH	Oberembrach	25	9	1988	460	ETHZ	
0	2	0	0	CH	ZH	Oetwil am See	11	10	1999	538	UGZ	Wohnung
0	1	0	0	CH	ZH	Oetwil am See	4	9	2000	538	UGZ	Haus
0	1	0	0	CH	ZH	Opfikon	18	7	2000	455	UGZ	Küche
0	1	0	0	CH	ZH	Otelfingen	18	10	1999	427	UGZ	Wohnung
0	2	0	0	CH	ZH	Otelfingen	18	10	1999	427	UGZ	Garten
1	0	0	0	CH	ZH	Otelfingen	20	6	2000	427	UGZ	Treppenhaus
1	0	0	0	CH	ZH	Pfäffikon	4	8	2000	540	UGZ	Wohnung
1	0	0	0	CH	ZH	Regensdorf	4	11	1999	460	UGZ	Haus
0	1	0	0	CH	ZH	Richterswil	17	11	1999	410	UGZ	Wohnung
0	1	0	0	CH	ZH	Richterswil	14	7	2000	410	UGZ	Haus/Estrich
1	1	1	0	CH	ZH	Richterswil	5	7	2000	410	UGZ	
0	1	0	0	CH	ZH	Schlieren	2	10	2000	390	UGZ	Haus
0	1	0	0	CH	ZH	Seegräben, Aathal, Linggenberg			2001	510	UGZ	
1	0	0	1	CH	ZH	Uitikon	17	7	2000	553	UGZ	Haus
1	0	0	0	CH	ZH	Uitikon, Waldegg	30	6	2000	620	UGZ	Bad/Küche
0	1	0	0	CH	ZH	Unterengstringen	29	9	2000	410	UGZ	Wohnung
0	1	0	0	CH	ZH	Urdorf	15	10	1999	420	UGZ	Küche
1	0	0	0	CH	ZH	Uster	11	9	1990	460	NMBE	Haus
1	0	0	0	CH	ZH	Uster	10	10	1993	460	NMBE	Haus
1	1	0	1	CH	ZH	Uster	23	9	1999	460	NMBE	Haus
0	1	0	0	CH	ZH	Uster	9	10	1999	460	NMBE	Haus
0	1	0	0	CH	ZH	Uster	31	10	1999	460	NMBE	Haus
2	1	1	0	CH	ZH	Uster		10	1999	460	NMBE	Haus
1	0	0	0	CH	ZH	Uster	5	6	2000	460	NMBE	Haus
0	1	0	0	CH	ZH	Uster	7	7	2000	460	UGZ	Haus
1	3	0	1	CH	ZH	Uster	19	8	2000	460	NMBE	Haus, 19.-23.8.2000
1	3	0	1	CH	ZH	Uster	23	8	2000	460	NMBE	Haus, 19.-23.8.2000
0	0	3	0	CH	ZH	Uster	4	9	2000	460	NMBE	Haus
0	0	3	0	CH	ZH	Uster	12	9	2000	460	NMBE	Haus
1	0	0	0	CH	ZH	Uster	27	9	2000	460	NMBE	Haus
2	1	0	0	CH	ZH	Uster		10	2000	460	NMBE	Haus
1	0	0	0	CH	ZH	Uster, Nänikon	8	8	2000	457	UGZ	Wohnung
2	1	0	0	CH	ZH	Volketswil	15	8	2000	465	UGZ	Haus und Umgebung
0	3	1	0	CH	ZH	Volketswil	21	8	2000	465	UGZ	
0	1	0	0	CH	ZH	Wädenswil	13	10	1999	500	UGZ	Haus

APPENDIX 2 (Fortsetzung)

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
1	3	1	1	CH	ZH	Wädenswil	28	9	2000	500	UGZ	Haus
4	3	4	1	CH	ZH	Wallisellen	14	9	2000	430	UGZ	Wohnung
0	1	0	0	CH	ZH	Weinigen, Fahrweid	5	7	2000	390	UGZ	Küche
0	1	0	0	CH	ZH	Wettswil am Albis	21	10	1999	562	UGZ	Haus
0	1	0	0	CH	ZH	Wetzikon		10	1999	530	NHMB	via "Deso Star" ans Museum gelangt
2	0	0	0	CH	ZH	Wetzikon	5	9	2000	530	UGZ	Haus
1	0	0	0	CH	ZH	Winterthur	20	8	1997	439	NMBE	Haus
1	0	0	0	CH	ZH	Winterthur	18	7	1999	439	NMBE	Wohnung
1	1	0	0	CH	ZH	Winterthur	6	8	1999	439	NMBE	Wohnung
0	1	0	0	CH	ZH	Winterthur	28	8	1999	439	NMBE	Wohnung
0	0	1	0	CH	ZH	Winterthur	5	9	1999	439	NMBE	Wohnung
1	0	0	0	CH	ZH	Winterthur	5	9	1999	439	NMBE	Wohnung
1	0	0	0	CH	ZH	Winterthur	7	9	1999	439	NMBE	Wohnung
1	0	0	0	CH	ZH	Winterthur	9	9	1999	439	NMBE	Wohnung
0	1	0	0	CH	ZH	Winterthur	8	10	1999	439	NMBE	Hauseingang
0	1	0	0	CH	ZH	Winterthur	14	10	1999	439	UGZ	Haus
0	2	0	1	CH	ZH	Winterthur	15	10	1999	439	UGZ	Schlafzimmer
0	0	1	0	CH	ZH	Winterthur	24	10	1999	439	NMBE	Wohnung
1	0	0	0	CH	ZH	Winterthur	1	11	1999	439	NMBE	auf <i>Prunus laurocerasus</i>
0	0	1	0	CH	ZH	Winterthur	14	12	1999	439	UGZ	Haus
0	0	1	0	CH	ZH	Winterthur	17	4	2000	439	NMBE	Hauseingang
1	2	0	0	CH	ZH	Winterthur	2	8	2000	439	UGZ	Haus und Umgebung
0	1	0	0	CH	ZH	Winterthur	9	8	2000	439	UGZ	Haus
1	1	0	0	CH	ZH	Zollikon	15	10	1999	480	UGZ	Büro
0	2	0	0	CH	ZH	Zürich		8	1992	411	ETHZ	
0	2	0	0	CH	ZH	Zürich	1	8	1995	411	ETHZ	
1	0	0	0	CH	ZH	Zürich	11	9	1995	411	ETHZ	
1	3	0	0	CH	ZH	Zürich	12	10	1996	411	NMBE	Hauseingang
0	0	1	0	CH	ZH	Zürich	17	9	1999	411	UGZ	Haus
1	2	0	0	CH	ZH	Zürich	17	9	1999	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	5	10	1999	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	15	10	1999	411	UGZ	Küchenschrank
0	1	0	0	CH	ZH	Zürich	28	10	1999	411	UGZ	Wohnung
0	0	1	0	CH	ZH	Zürich	11	11	1999	411	UGZ	Haus
1	0	0	0	CH	ZH	Zürich	11	11	1999	411	UGZ	Haus
0	0	1	0	CH	ZH	Zürich	19	11	1999	411	UGZ	Geranien
0	0	1	0	CH	ZH	Zürich	9	3	2000	411	UGZ	Hausmauer
0	0	1	0	CH	ZH	Zürich	5	5	2000	411	UGZ	Wohnung
0	0	1	0	CH	ZH	Zürich	16	6	2000	411	UGZ	Haus
1	0	3	0	CH	ZH	Zürich	22	6	2000	411	UGZ	
2	0	0	0	CH	ZH	Zürich	22	6	2000	411	UGZ	
2	1	1	0	CH	ZH	Zürich	26	6	2000	411	UGZ	Haus und Umgebung
1	0	0	0	CH	ZH	Zürich	27	6	2000	411	UGZ	Küche
1	0	0	0	CH	ZH	Zürich	7	7	2000	411	UGZ	Haus
0	1	2	0	CH	ZH	Zürich	10	7	2000	411	UGZ	Haus
2	0	0	0	CH	ZH	Zürich	17	7	2000	411	UGZ	Waschküche
0	1	0	0	CH	ZH	Zürich	17	7	2000	411	UGZ	
2	0	0	0	CH	ZH	Zürich	19	7	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	20	7	2000	411	UGZ	Restaurant
1	0	0	0	CH	ZH	Zürich	24	7	2000	411	UGZ	Fenstersims
1	0	0	0	CH	ZH	Zürich	24	7	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	25	7	2000	411	UGZ	Wohnung
3	1	1	0	CH	ZH	Zürich	28	7	2000	411	UGZ	Wohnung und auf Balkon
3	1	0	0	CH	ZH	Zürich	2	8	2000	411	UGZ	Wohnung
1	3	0	0	CH	ZH	Zürich	2	8	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	3	8	2000	411	UGZ	Küche
0	1	0	0	CH	ZH	Zürich	3	8	2000	411	UGZ	Treppenhaut
0	4	0	0	CH	ZH	Zürich	3	8	2000	411	UGZ	
0	1	0	0	CH	ZH	Zürich	7	8	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	8	8	2000	411	UGZ	Wohnung
3	2	1	0	CH	ZH	Zürich	9	8	2000	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	9	8	2000	411	UGZ	Haus
2	2	1	0	CH	ZH	Zürich	10	8	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	10	8	2000	411	UGZ	Wohnung
0	2	0	0	CH	ZH	Zürich	15	8	2000	411	UGZ	Haus

APPENDIX 2 (Ende)

♂	♀	Ny	Oo	Ld	Kt	Ort	Tag	Mon	Jahr	Höhe	Coll.	Bemerkungen
0	1	0	0	CH	ZH	Zürich	16	8	2000	411	UGZ	Haus
6	1	0	0	CH	ZH	Zürich	16	8	2000	411	UGZ	Wohnung
0	1	0	0	CH	ZH	Zürich	17	8	2000	411	UGZ	Wohnung
0	2	0	0	CH	ZH	Zürich	18	8	2000	411	UGZ	Buffet der Badeanstalt (offen)
0	1	0	0	CH	ZH	Zürich	22	8	2000	411	UGZ	Wohnung
0	2	0	0	CH	ZH	Zürich	25	8	2000	411	UGZ	Haus und Umgebung
0	1	0	0	CH	ZH	Zürich	25	8	2000	411	UGZ	Wohnung
2	0	0	0	CH	ZH	Zürich	25	8	2000	411	UGZ	
0	1	0	0	CH	ZH	Zürich	28	8	2000	411	UGZ	Wohnung
1	1	0	0	CH	ZH	Zürich	31	8	2000	411	UGZ	Haus
0	0	1	0	CH	ZH	Zürich	31	8	2000	411	UGZ	
0	1	0	0	CH	ZH	Zürich	5	9	2000	411	UGZ	Wohnung
1	6	0	1	CH	ZH	Zürich	13	9	2000	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	20	9	2000	411	UGZ	Haus
0	2	0	1	CH	ZH	Zürich	21	9	2000	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	27	9	2000	411	UGZ	
0	1	0	0	CH	ZH	Zürich	28	9	2000	411	UGZ	Hotel
1	0	1	0	CH	ZH	Zürich	20	10	2000	411	UGZ	Wohnung
0	0	1	0	CH	ZH	Zürich	25	10	2000	411	UGZ	Wohnung, Toilette
0	1	0	1	CH	ZH	Zürich	26	10	2000	411	UGZ	Küche
0	1	0	0	CH	ZH	Zürich	26	10	2000	411	UGZ	Wohnung
1	0	0	0	CH	ZH	Zürich	3	11	2000	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	8	11	2000	411	UGZ	Haus
0	4	0	0	CH	ZH	Zürich	13	11	2000	411	UGZ	Haus
0	1	0	0	CH	ZH	Zürich	14	11	2000	411	UGZ	Küche
0	0	1	0	CH	ZH	Zürich	28	11	2000	411	UGZ	Küche
0	1	0	1	CH	ZH	Zürich	29	11	2000	411	UGZ	Haus
0	0	1	0	CH	ZH	Zürich, Affoltern	24	5	2000	460	UGZ	Wohnzimmer und Küche
0	0	1	0	CH	ZH	Zürich, Albisrieden	13	4	2000	450	UGZ	Balkon
0	0	1	0	CH	ZH	Zürich, Albisrieden	24	4	2000	450	UGZ	Balkon
1	0	0	0	CH	ZH	Zürich, Altstetten	8	6	2000	440	UGZ	Küche
0	0	1	0	CH	ZH	Zürich, Altstetten	16	6	2000	440	UGZ	Balkon
1	0	0	0	CH	ZH	Zürich, Altstetten	21	6	2000	440	UGZ	Haus
1	0	0	0	CH	ZH	Zürich, Altstetten	22	6	2000	440	UGZ	Schlafzimmer
0	0	1	0	CH	ZH	Zürich, Höngg	17	10	2000	500	UGZ	Wohnung, Küche
2	0	0	0	CH	ZH	Zürich, Oerlikon	20	9	1999	465	UGZ	Haus
2	0	0	0	D	BW	Bad Krozingen	8	2002		NHMB	Wohnhaus	
0	0	0	0	D	BW	Gottenheim, NW Freiburg i.Br.		2002		NHMB	Siedlung; 3 Ex. (keine Belege)	
1	0	0	0	D	BW	Lörrach	7	2002		NHMB	Wohnhaus	
0	1	1	0	D	BW	Weil am Rhein	10	2001	270	NHMB	Tierhandlung, gehäuftes Auftreten	
1	0	0	0	I	NI	Bellagio, S.S. Giovanni/Como	19	7	1981		CAN	
0	2	0	0	I	NI	Chiavenna, SSE Grat M. Matec	1	9	1971	1000	CAN	950-1050 m
1	0	0	0	I	NI	Dorio, Ronchi Vesgallio/Como	12	8	1963	350	CAN	250-450 m
1	0	0	0	I	NI	Mendotica/Ligurien	14	8	1986	880	CAN	
0	1	0	0	I	NI	Pamparato, S.Grée/Piemonte	2	9	1985	1125	CAN	1100-1150 m
1	2	0	0	I	NI	Portese-Salò/Gardasee	22	8	1921		ZMB	Syntypen <i>E. vitreus</i> Ramme
0	1	0	0	I	NI	Savogno/Friaul	26	8	1973	350	CAN	200-500 m
1	0	0	0	I	NI	Sondrio, Albionico, Il Forno	22	7	1981	575	CAN	550-600 m
1	0	0	0	I	NI	Sondrio, Olgiasca-Piona	21	7	1981	311	CAN	250-372 m
1	0	0	0	I	NI	Vatgumnu	18	7	1959		CAN	Sumpfwiese
0	1	0	0	I	NI	Vestreno, Mad. Bondo/Como	6	9	1963	600	CAN	
29	0	0	0	I	TO	S. Gimignano, 4,5km ESE	4	9	1997	130	NMBE	

***Amblyrhynchichthys micracanthus*, a new species of cyprinid fish from Indochina (Cypriniformes: Cyprinidae)**

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***Amblyrhynchichthys micracanthus*, a new species of cyprinid fish from Indochina (Cypriniformes: Cyprinidae).** - *Amblyrhynchichthys micracanthus* sp. n. is described from the Mekong, Chao Phraya, Mae Khlong and Tapi river drainages in Indochina (mainland Southeast Asia). It can be distinguished from its only congener, *A. truncatus*, in having a more truncate snout (with a straight vs. gently rounded lateral profile), shorter dorsal spine (15.5–25.7 %SL vs. 26.7–29.9), smaller eye when similar-sized individuals of larger than ca. 70 mm SL are compared (28.7–34.9 %HL vs. 32.7–36.3), and fewer gill rakers (34–37 vs. 39–40).

Key-words: *Amblyrhynchichthys* - Cyprinidae - new species - Indochina.

INTRODUCTION

Fishes of the cyprinid genus *Amblyrhynchichthys* Bleeker, 1860 (type species *Barbus truncatus* Bleeker, 1851) are easily distinguished from other cyprinids in having an extremely blunt snout, anteriorly situated nostrils, last simple dorsal-fin ray stout and serrated posteriorly, and a well-developed hyaline eyelid. To date, the genus has been considered monotypic, being found in river drainages throughout Sumatra, Borneo and Indochina (mainland Southeast Asia). The other nominal species referred to *Amblyrhynchichthys*, *A. altus* Vaillant, 1893, is considered a junior synonym of *Kalimantania lawak* (Bleeker, 1855) (see Bănărescu, 1980).

A comparison of Indochinese, Sumatran and Bornean specimens previously identified as *A. truncatus* shows that two distinct species can be recognised, with the Indochinese one described herein as *Amblyrhynchichthys micracanthus*. In previous literature on Indochinese fishes (e.g. Roberts & Warren, 1994: 100; Rainboth, 1996: 86, Pl. VII Fig. 50; Kottelat, 2001: 38, Fig. 25), *A. micracanthus* has been identified as *A. truncatus* (type locality: Banjarmasin in southern Borneo). The situation in *Amblyrhynchichthys* is one more example of a species once considered to have a very wide distribution in large rivers throughout Southeast Asia and now found to consist of two distinct species: one Sundaic (Borneo, Java, Sumatra and Malay Peninsula) and one northern Indochinese (Mekong and Chao Phraya basins). Other cases reported in

recent years include: *Belodontichthys dinema* and *B. truncatus*, *Laides hexanema* and *L. longibarbis*, *Bagrichthys macropterus* and *B. obscurus*, and *Helicophagus waandersii* and *H. leptorhynchus* (Kottelat & Ng, 1999; Ng 1999a, b; Ng & Kottelat, 2000) and we are aware of numerous other cases awaiting re-analysis. A model of the historical biogeography of species with this pattern of distribution has been proposed by Bornbusch & Lundberg (1989), who hypothesized that the post-Pleistocene isolation of the North Sunda River system resulted in speciation.

MATERIAL AND METHODS

Measurements were made point to point with dial callipers and data recorded to 0.1 mm. Counts and measurements were made on the left side of specimens whenever possible. Subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of body parts are given as proportions of standard length (SL). Measurements and counts were made following Hubbs & Lagler (1947), except for scale counts, which follow those of Kottelat (1984, 1990), and pharyngeal tooth counts, which follow those of Jenkins & Burkhead (1994), but exclude the replacement teeth.

Fin rays were counted under a binocular dissecting microscope using transmitted light. Material for this study is deposited in the following collections: California Academy of Sciences, San Francisco (CAS), collection of the second author, Cornol (CMK), Museum of Comparative Zoology, Cambridge (MCZ), Nationaal Natuurhistorisch Museum, Leiden (RMNH), Museum of Zoology, University of Michigan, Ann Arbor (UMMZ), and the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, Singapore (ZRC).

DESCRIPTION

Amblyrhynchichthys micracanthus sp. n.

Figs 1 and 2a

Holotype. UMMZ 232203, 100.2 mm SL; Cambodia: Kandal province, Tonle Sap River 22 km upstream from Phnom Penh; W. J. Rainboth and N. van Zalinga, 16 January 1995.

Paratypes. CAMBODIA: CAS 94193, 1 ex., 111.8 mm SL; market at Phnom Penh; T. R. Roberts and K. E. Witte, 18 January–20 February 1994. CAS 94285, 5 ex., 98.0–125.3 mm SL; Cambodia: Stung Treng; T. R. Roberts, 2–18 February 1994. UMMZ 181245, 2 ex., 97.0–122.2 mm SL; Pursat province, Great Lake at Kompong Luong; J. Bardach, 18 March 1959. UMMZ 232277, 1 ex., 103.3 mm SL; Stung Treng morning market; W. J. Rainboth, N. van Zalinga and C. Rotha, 26 January 1995. UMMZ 232527, 2 ex., 101.6–110.2 mm SL; Kandal province, Tonle Sap; W. J. Rainboth and C. Rotha, 13 February 1995. UMMZ 232622, 1 ex., 68.5 mm SL; Kandal province, Prek Mong Ya, just upstream from confluence with Bassac River at fishing lot 10; W. J. Rainboth and C. Rotha, 20 February 1995. UMMZ 232713, 1 ex., 91.5 mm SL; Kompong Thom province, Tonle Sap at exit to Great Lake, 4 km NW of Chhnok Trou, at Kompong Thom fishing lot 2; W. J. Rainboth, N. van Zalinga and C. Rotha, 28 February 1995. UMMZ 234374, 1 ex., 97.2 mm SL; Kandal province, Tonle Sap at Dai fishery row 9, 25 km upstream from Phnom Penh; W. J. Rainboth *et al.*, 22 January 1996. UMMZ 235499, 3 ex., 79.3–91.5 mm SL; Kandal province, Tonle Sap at Dai fishery row 9, 15 km upstream from Phnom Penh; W. J. Rainboth *et al.*, 27 January 1996. LAOS: CAS 94272, 1 ex., 102.4 mm SL; Champasak province, Mekong river at Ban Hang Khone, just below Khone Falls; T. R. Roberts, June–July 1993. CMK 13137, 6 ex., 59.4–68.1 mm SL; Vientiane province, Mekong River at mouth of Nam Mang and lower 100 m of Nam Mang, 18°21'48"N 103°14'16"E; M. Kottelat *et al.*, 22 February 1997. UMMZ 235320, 2 ex., 135.8–170.6 mm SL; Champasak province,

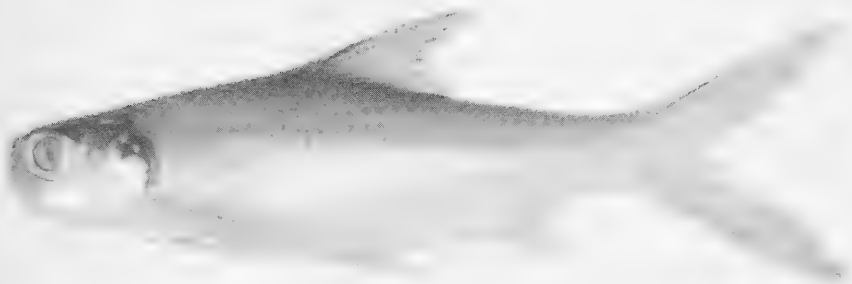


FIG. 1

Amblyrhynchichthys micracanthus, CMK 13137, paratype, 68.1 mm SL.

Mekong River at Ban Hang Khone, just downstream from Khone Falls; I. G. Baird, date unknown. THAILAND: CAS 61877, 2 ex., 128.1-141.4 mm SL; Ubon Ratchathani province, fish market at Ubon Ratchathani; T. R. Roberts, 28 June 1985. CAS 93243, 1 ex., 95.8 mm SL; Ayutthaya province, Ayutthaya market; T. R. Roberts, 5-7 March 1989. CAS 93921, 2 ex., 95.9-144.7 mm SL; Nakhon Sawan province, Nakhon Sawan market; T. R. Roberts, 4-5 February 1989. MCZ 47307, 165.2 mm SL; Mekong River at Nong Khai; T. R. Roberts, May 1970. UMMZ 195088, 1 ex., 125.1 mm SL; Nakhon Sawan province, Chao Phraya River, floodwaters 20 km N of Nakhon Sawan; K. F. Lagler, 15 October 1964. UMMZ 195364, 39 mm SL; Maharaj province, Chao Phraya River, 17.5 km N of Ayutthaya; S. Mekbahn, 27 December 1964. UMMZ 195856, 1 ex., 98.5 mm SL; Mae Nam Khwae Yai about 10 km upstream from Kanchanaburi; K. F. Lagler, 24 March 1965. UMMZ 195883, 5 ex., 84.3-168.1 mm SL; Mae Nam Mae Khlong at 2 km downstream of Ban Pong; K. F. Lagler *et al.*, 25 March 1965.

Non-types. CAMBODIA: UMMZ 234483, 2 ex., 36.1-51.2 mm SL; Kandal province, floodplain lake near Mekong. THAILAND: UMMZ 185226, 1 ex., 94.3 mm SL; vicinity of Bangkok. UMMZ 195396, 17 ex., 35.3-53.3 mm SL; Maharaj province, Kok Tong Canal (tributary of Chao Phraya River) 17.5 km N of Ayutthaya. UMMZ 195722, 4 ex., 62.9-73.5 mm SL; Ubon Ratchathani province, Mun River, about 20 km downstream from Ubon Ratchathani. UMMZ 195739, 1 ex., 64.1 mm SL; Ubon Ratchathani province, Mun River, about 5 km downstream from Ubon Ratchathani. UMMZ 224265, 1 ex., 101.3 mm SL; Ubon Ratchathani province, Khong Chiam district, Mun River at Ban Dan, 1.2 km upstream from confluence with Mekong River. UMMZ 224296, 1 ex., 114.7 mm SL; Nakhon Phanom province, Mekong River, island off Ban Tha Kai, 20 km downstream from Mukdahan, 1 km from Thai, 5 km from Laos side. UMMZ 224311, 1 ex., 111.5 mm SL; UMMZ 224353, 1 ex., 128.4 mm SL; UMMZ 224364, 1 ex., 137.7 mm SL; UMMZ 224391, 1 ex., 132.9 mm SL; UMMZ 224398, 1 ex., 121.6 mm SL; UMMZ 224448, 2 ex., 114.7-196.7 mm SL; UMMZ 224455, 1 ex., 111.5 mm SL; Ubon Ratchathani province, Khong Chiam district, Mun River at Ban Dan, 3 km upstream from confluence with Mekong River. UMMZ 224508, 1 ex., 95.8 mm SL; Ubon Ratchathani province, stream from Bung Klang Huen to Mun River, 10 km from Mun River, 3 km E of Ubon Ratchathani. UMMZ 233820, 1 ex., 43.0 mm SL; Ubon Ratchathani province, Huay Mark, 8 km N of Khong Chiam at confluence with Mekong River. UMMZ 237228, 30 ex., 36.2-58.7 mm SL; Maharaj province, Kok Tong, 15 km N of Ayutthaya, tributary of Lop Buri and Chao Phraya rivers. VIETNAM: UMMZ 218147, 13 ex., 29.0-59.1 mm SL; Phong Dinh province, Bassac

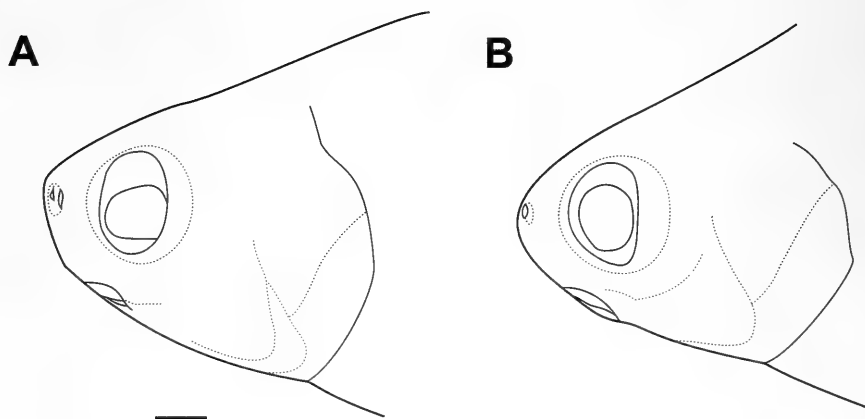


FIG. 2

Lateral views of heads of: A. *Amblyrhynchichthys micracanthus*, UMMZ 235320, paratype, 135.8 mm SL; B. *A. truncatus*, CMK 4763, 137.8 mm SL. Scale bar indicates 5 mm.

River 0.5 km downstream from Can Tho. UMMZ 218533, 9 ex., 27.2-47.2 mm SL; UMMZ 218547, 19 ex., 31.0-48.8 mm SL; UMMZ 218568, 11 ex., 26.5-43.1 mm SL; UMMZ 218583, 1 ex., 49.5 mm SL; Phong Dinh province, Bassac River at Can Tho. UMMZ 218675, 8 ex., 40.8-73.0 mm SL; Phong Dinh province, Bassac River adjacent to Dong Phu. UMMZ 218651, 91 ex., 24.0-62.2 mm SL; An Giang province, Bassac River 1.3 km S of Long Xuyen. UMMZ 224853, 1 ex., 49.5 mm SL; An Giang province, rice paddy 1 km S of Highway 10 in Hoa Binh Thanh district. UMMZ 224956, 1 ex., 97.5 mm SL; Phong Dinh province, Can Tho fish market.

Diagnosis. *Amblyrhynchichthys micracanthus* can be distinguished from its sole congener, *A. truncatus*, in having a more truncate snout (with a straight vs. gently rounded lateral profile), shorter dorsal spine (15.5-25.7 %SL vs. 26.7-29.9), smaller eye when similar-sized individuals of larger than ca. 70 mm SL are compared (28.7-34.9 %HL vs. 32.7-36.3), and fewer gill rakers (34-37 vs. 39-40).

Description. Morphometric and meristic data are given in Table 1. Body moderately deep and strongly compressed, with narrow predorsal midline. Predorsal profile smoothly rounded, with small concavity at nape and then sloping gently ventrally from origin of dorsal fin to end of caudal peduncle. Ventral profile less convex than dorsal profile, sloping gently ventrally to anterior end of anal-fin base, then sloping more steeply dorsally from there to end of caudal peduncle. Lateral line complete. Scales with strongly convergent radii.

Head narrow, snout extremely blunt, with a vertical lateral profile. Nostrils large and anteriorly situated. Eye in upper half of head, visible from dorsal and ventral aspects; moderately large. Hyaline eyelid well developed, covering anterior and posterior quarters of orbit. Suborbital bones fairly large, narrowest directly below eye. Mouth subterminal, with well-developed groove separating lips from both upper and lower jaws. Lips thick; lower lip present medially and with complete post-labial groove. Gill membranes broadly joined to isthmus. Gill rakers long, one third as long as opposing filaments on epibranchial and half as long as opposing filaments on ceratobranchial. Pharyngeal bones stout, with three rows (2,3,4-4,3,2) of curved,

TABLE 1. Morphometric and meristic data for *Amblyrhynchichthys micracanthus* (n=30: 35.7–170.6 mm SL)

MORPHOMETRICS		MERISTICS	
In %SL			
Head length	23.5–28.6	Dorsal-fin rays	iv,9 (30)
Head width	12.0–16.4	Anal-fin rays	iii,5 (30)
Head depth	16.9–20.6	Pelvic-fin rays	i,8 (30)
Body depth at dorsal origin	24.4–36.3	Pectoral-fin rays	i,14 (30)
Predorsal length	46.8–50.9	Caudal-fin rays	i,9,8,i (30)
Preanal length	70.6–77.2	Lateral line scales	35+2 (30)
Prepelvic length	43.9–49.6	Predorsal scales	11 (30)
Prepectoral length	23.5–27.5	Scales in transverse lines	1/25/1/3 1/2 (30)
Length of dorsal-fin base	14.6–19.1	Circumpeduncular scales	1/23/1/3 1/2 (30)
Dorsal-spine length	15.5–25.7	Rakers on first gill arch	10+24 (9),
Anal-fin length	9.2–11.4		11+23 (3),
Pelvic-fin length	17.6–21.0		10+25 (7),
Pectoral-fin length	18.2–20.1		11+24 (3),
Caudal-fin length	24.2–31.2		10+26 (3),
Length of caudal peduncle	16.2–21.0		11+25 (3) or
Depth of caudal peduncle	7.6–13.0		10+27 (2)
In %HL		Vertebrae	20+12=32 (4) or
Snout length	22.0–28.0		20+13=33 (26)
Interorbital distance	21.1–39.9		
Eye diameter	28.7–34.9		

chisel-shaped teeth. Grinding surfaces of distalmost major teeth widest, width progressively decreasing proximally.

Dorsal fin moderately high, with concave distal margin, sharply pointed at apex; origin slightly anterior to pelvic-fin origin. Last unbranched ray longest; spinous part with 11 to 18 serrations on posterior edge. Pectoral fin long and falcate, extending to scale row at pelvic-fin origin; distal margin concave near tip but straight otherwise. Pelvic fin moderately falcate, extending to slightly more than midway between pelvic-fin origin and anterior base of anal-fin; distal margin nearly straight. Anal fin with strongly concave distal margin and last three posterior rays equal in length; when adpressed against body, extending to middle of caudal peduncle. Two scale rows between urogenital opening and anal-fin origin. Caudal peduncle strongly compressed and moderately long. Caudal fin deeply forked, upper and lower lobes pointed.

Sexual dimorphism absent. Breeding tubercles absent and body depth between sexes not different.

Colour. Preserved material with a pale brown body and a faint broad stripe consisting of aggregations of melanophores on sides of body immediately above lateral line. Dorsal and caudal fins hyaline, with a faint black posterior margin. All other fins hyaline. Colour in life an overall silvery white.

Distribution. Lower and middle Mekong, Chao Phraya, Mae Khlong and Tapi river drainages in Indochina (mainland Southeast Asia). In the Mekong, it reaches upriver to Vientiane.

Etymology. From the Greek mikros, meaning small, and akantha, meaning thorn. In reference to the smaller dorsal spine of this species compared to *A. truncatus*. Treated as an adjective.

Ecology. *Amblyrhynchichthys micracanthus* is found mainly in rivers, with juveniles occasionally entering swamps and flooded fields (Taki, 1978). In the Mekong River drainage, this species moves into the inundated forest during the flood season (June–September) and return to the river in October and November (Rainboth, 1996). It feeds mainly on periphyton; other minor food items include phytoplankton, zooplankton and benthic algae (Rainboth, 1996).

DISCUSSION

The difference in eye diameter between *A. micracanthus* and *A. truncatus* is only apparent when similar-sized individuals are compared. We were able to examine only two specimens smaller than 90 mm SL for *A. truncatus*, but when eye diameter is plotted against SL for both species (Fig. 3), the graph indicates that the comparison is only meaningful when specimens of the same size (larger than ca. 70 mm SL) are used.

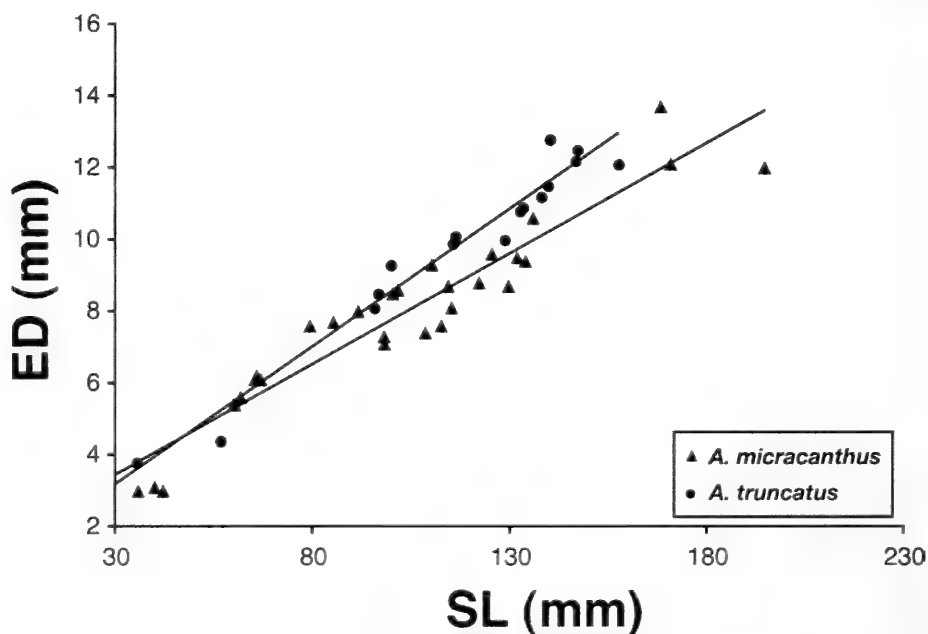


FIG. 3

Eye diameter (ED) plotted against standard length for *Amblyrhynchichthys* species.

The morphometric differences observed between *A. micracanthus* and *A. truncatus* cannot be explained by ontogeny alone. The regression lines in the biplots of eye diameter (Fig. 3) and dorsal-spine length (Fig. 4) against SL show are significantly different (ANCOVA, $P=0.00111$ and $P<0.0000005$ respectively).

Although the different snout shapes of *A. truncatus* and *A. micracanthus* would suggest that the shapes of the maxilla, premaxilla and possibly the circumorbital bones would differ, no significant differences in the osteology of the two species were observed, suggesting that the differences in shape are more likely caused by soft tissue.

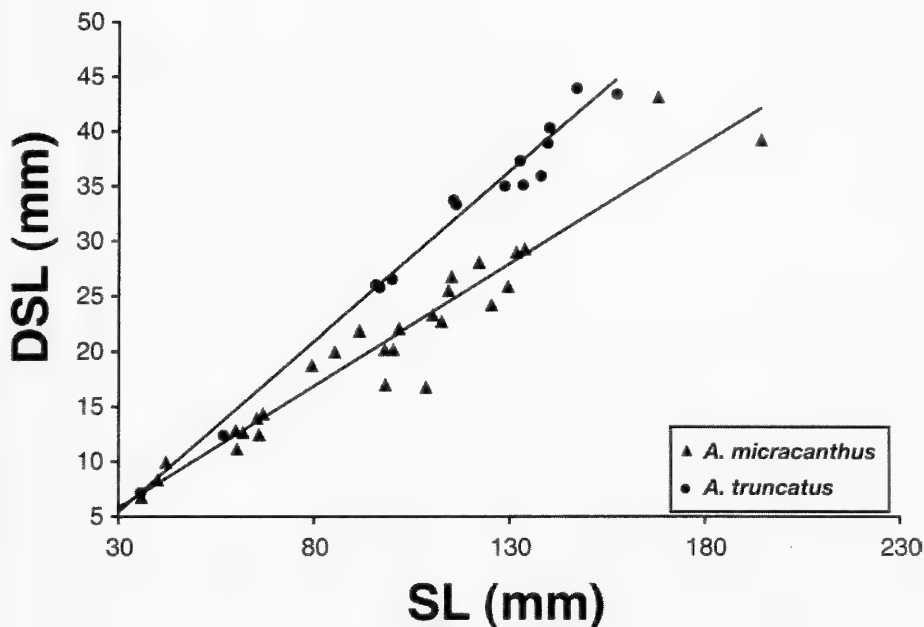


FIG. 4

Dorsal-spine length (DSL) plotted against standard length for *Amblyrhynchichthys* species.

Bleeker (1851) described *A. truncatus* on the basis of three specimens 50–110 mm TL [total length] from Banjarmasin, Borneo. We have examined 2 specimens from Bleeker's collection which were registered as syntypes. RMNH 9091 is 35.3 mm SL, which corresponds to a total length of 50 mm and therefore seems to be the 50 mm TL syntype. RMNH 7032 is 56.5 mm SL and is probably the third specimen, for which Bleeker did not indicate the size (between 50 and 110 mm TL). Other Bleeker specimens of *A. truncatus* in RMNH are too large to be syntypes (RMNH 17176, 4, 96.5–203.4 mm SL; the 96.5 mm SL specimen would have been at least 120 mm TL). The whereabouts of the third syntype are not known. The 'cotype' listed by Bertin & Estève (1948) cannot have a type status as it is too large and is from Sumatra. The two syntypes agree with *A. truncatus* as diagnosed above and RMNH 9091 is hereby designated as lectotype.

COMPARATIVE MATERIAL

Amblyrhynchichthys truncatus: BORNEO: RMNH 7032, paralectotype, 56.5 mm SL; RMNH 9091, lectotype, 35.3 mm SL; Kalimantan Selatan, Banjarmasin. CMK 10190, 2 ex., 116.1–157.3 mm SL; Kalimantan Barat, Danau Genting, between Danau Pengembung and Danau Belida. UMMZ 209912, 2 ex., 95.5–115.4 mm SL; Kalimantan Barat, Sungai Tawang near Danau Pengembung. ZRC 40025, 1 ex., 146.5 mm SL; Kalimantan Selatan, Banjarmasin, Pasar Lima Beton. SUMATRA: CMK 4763, 2 ex., 133.2–137.8 mm SL; ZRC 38556, 1 ex., 147.0 mm SL; ZRC 43160, 2 ex., 132.4–140.0 mm SL; ZRC 44109, 2 ex., 128.5–139.5 mm SL; Jambi, Pasar Angso Duo. MALAY PENINSULA: ZRC 1764, 1 ex., 175.8 mm SL; Malaysia: Pahang, King George V National Park. ZRC 1765, 1 ex., 173.0 mm SL; Malaysia: Pahang, Kuala Tahan.

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The centipedes of the Maltese Archipelago (Chilopoda)

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The centipedes of the Maltese Archipelago (Chilopoda). - The chilopod fauna of the Maltese Islands (Malta, Gozo, Comino) was studied from a faunistic and zoogeographic point of view. A list of the species found on these islands is given, based on recent faunistic investigations as well as on a critical assessment of the few records available in the literature. Twenty-one species are recorded to occur on the islands: 1 Scutigermorpha, 7 Lithobiomorpha, 3 Scolopendromorpha, and 10 Geophilomorpha. Twenty species are confirmed to occur on the island of Malta, 11 on Gozo and three on Comino. The Maltese chilopod fauna mostly consists of species that are widespread in the Mediterranean islands, particularly those of the western Mediterranean. As shown in other studies on the chilopod faunas of other Mediterranean micro-insular systems, that of the Maltese Islands is mainly influenced by ecological factors rather than by paleogeographic and paleoclimatic ones. Zoogeographically the Maltese chilopod fauna is mainly Mediterranean in character, with a very limited representation of Holarctic (22%) and European (11%) species.

Key-words: Chilopoda - Maltese Islands - Malta - Gozo - Comino - fauna - biogeography.

INTRODUCTION

Very few papers have been devoted to the Maltese centipedes so far. The first lists of species were published at the end of the nineteenth century by the Maltese naturalist Giovanni Gulia (Gulia, 1890, 1913), who recorded only three species, all probably collected and studied by himself. About eighty years later, Matic *et al.* (1967) listed another seven species from material collected in 1965 by Marcello La Greca and co-workers, as part of a research programme on the Mediterranean fauna carried out by the Zoological Institute of the University of Catania (Italy). After that, the only published work on this subject known to us is a list of 12 species from the Maltese Islands, in a study on the centipede fauna of the West Mediterranean area by Foddai *et al.* (1996).

Recently (mainly in the eighties), research on the Maltese fauna has been taken up by workers from the University of Malta and ample material has been collected from the main islands of the archipelago. This material, together with specimens occasionally collected by Italian universities and natural history museums, is the subject of the present study.

The aim of this paper is to list and discuss this material and all the previously published records of chilopods from the Maltese islands.

STUDY AREA

The Maltese archipelago (Fig. 1), situated in the central Mediterranean, approximately 96 km from Sicily and 290 km from North Africa, consists of three inhabited islands, i.e. Malta (246.5 km²), Gozo (65.8 km²) and Comino (2.9 km²) and of a number of small uninhabited islets (each less than 10 ha). The islands are mainly composed of Oligo-Miocene limestones, the soils are young and very similar to the parent rocks, and there are no mountains, streams or lakes, but only minor springs. The climate is typically Mediterranean and strongly bi-seasonal: the average annual rainfall is c. 530 mm, of which some 85% falls during the period October to March; the mean monthly temperature range is 12–26°C, and the islands are very windy and sunny. The main geomorphological features are karstic limestone plateaux, hillsides covered with clay taluses, gently rolling limestone plains, valleys (*widien*, see below) that drain runoff during the wet season, steep sea-cliffs on the south-western coasts, and gently sloping rocky shores to the Northeast. The islands have been more or less continuously inhabited since 7000 BP and human impact is significant. Presently some 38% of the land area is cultivated, c. 25% is built up, and the rest is countryside.

The terrestrial habitats of the Maltese Islands are mainly characterized by the vegetation which can be grouped in three categories: (i) communities that are part of the successional sequence (steppe, garigue, maquis) towards a climax (sclerophyll forest); (ii) communities which are either specialised to occupy particular habitats, or occupy habitats that are rare on the islands, or are relics from a previous ecological regime, now surviving in a few refugia; and (iii) vegetational assemblages of disturbed habitats, occupying land subject to periodic disturbance, usually related to anthropic activities.

It is thought that before humans colonised the Maltese Islands, large areas were covered with a Mediterranean sclerophyll forest characterised by *Quercus ilex* and *Pinus halepensis*. The early settlers cut the trees for wood and to clear the land for agriculture and buildings, and introduced sheep and goats whose grazing and browsing prevents the trees from regenerating. The native forest on the Maltese Islands is all but extinct and only remnants persist at four localities, none of which has more than a few dozen trees. More extensive tree-covered areas nonetheless exist on the islands; however, all owe their origin to human activities (e.g., gardens, plantations, orchards etc.). Although originally planted, some are now self-maintaining and self-regenerating, and therefore qualify as semi-natural woodlands.

The Maltese maquis is an impoverished scrub community resulting from degeneration of the climax woodland due to cutting, grazing and erosion of the soil. A

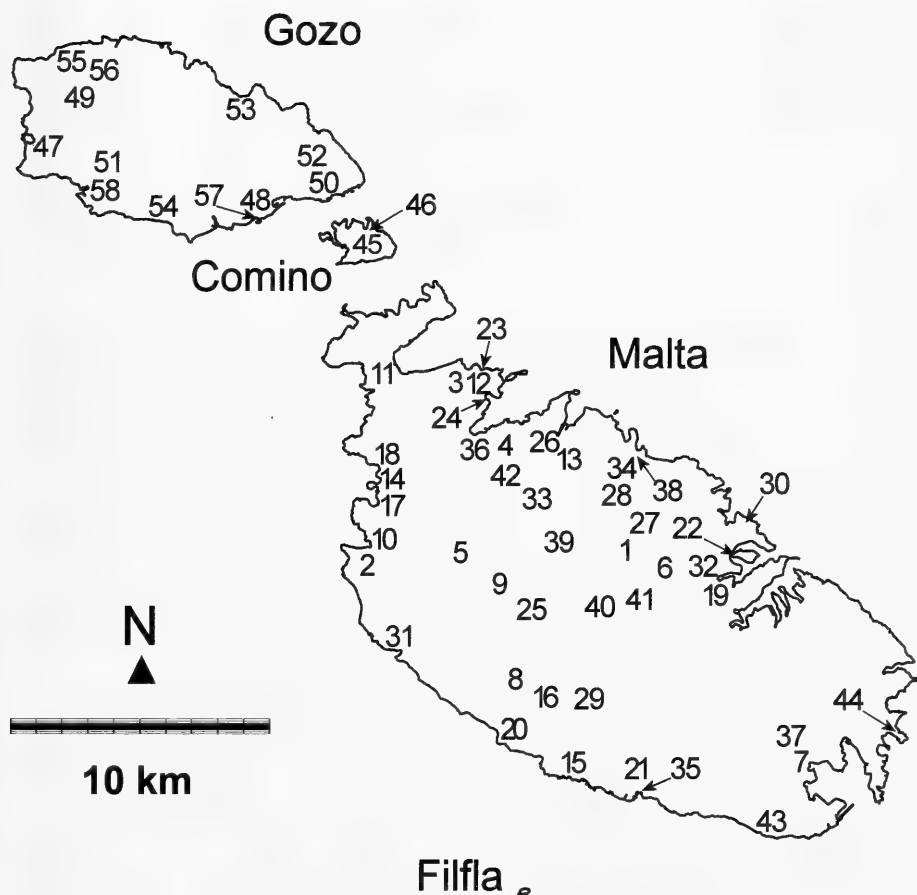


FIG. 1

Map of the Maltese Islands showing the localities from where centipedes recorded in this paper were collected. Key (in alphabetical order): **Malta**: 1 Attard, 2 Bahrija (Wied tal-Bahrija), 3 Ballut ta' l-Imgiebah, 4 Ballut tal-Wardija/Wardija, 5 Bingemma Gap, 6 Birkirkara, 7 Borg in-Nadur (Birzebbuga), 8 Buskett, 9 Chadwick Lakes, 10 Fomm ir-Rih, 11 Ghadira, 12 Ghajn Hadid (Selmun), 13 Ghajn Rihana, 14 Ghajn Tuffieha, 15 Ghar Lapsi, 16 Girgenti, 17 Gnejna, 18 Golden Bay, 19 Gwardamangia, 20 Il-Fawwara (Dingli Cliffs), 21 Il-Maqluba (Qrendi), 22 Manoel Island, 23 Mgiebah Bay, 24 Mistra Bay/Tal-Kortin, 25 Rabat (St. Agatha's Catacombs), 26 Salina, 27 San Anton Gardens, 28 San Pawl tat-Targa, 29 Siggiewi, 30 Sliema, 31 Ta' Hammud (Mtahleb), 32 Tal-Qroqq (UOM), 33 Targa Gap, 34 Wied Anglu, 35 Wied Babu, 36 Wied Bufula, 37 Wied Hassabtan, 38 Wied il-Faham, 39 Wied il-Ghasel (Mosta), 40 Wied Incita, 41 Wied is-Sewda, 42 Wied Qannotta, 43 Wied Znuber, 44 Xrobb l-Ghagin; **Comino**: 45 Central area, 46 Santa Marija Bay; **Gozo**: 47 Dwejra, 48 Fort Chambray slopes, 49 Gharb, 50 Hondoq ir-Rummien, 51 Kercem, 52 Qala, 53 Ramla, 54 Ta' Cenc, 55 Wied ic-Cawla, 56 Wied il-Mielah, 57 Xatt l-Ahmar, 58 Xlendi.

semi-natural maquis survives in relatively inaccessible sites, such as the sides of steep valleys, and at the foot of escarpments, while an artificial maquis develops round previously cultivated trees, mainly *Olea europaea* and *Ceratonia siliqua*.

The most widespread natural vegetation type present is the garigue. Some garigue communities are natural, others result from degradation of forest and maquis, particularly where removal of the original vegetation cover has caused such extensive soil erosion that large tracts of the limestone bedrock have become exposed and only patches of stony soil still occur. Garigues are typical of such rocky ground and are especially common on the flat karstic limestone platforms of western Malta and the Gozitan hills. Many subtypes of Maltese garigue exist; the principal ones are those dominated by *Coridothymus capitatus*, *Anthyllis hermanniae*, *Teucrium fruticans*, *Erica multiflora*, and the endemic *Euphorbia melitensis*; mixed garigues dominated by two, three or more of these species are also common.

Steppic assemblages dominated by grasses, umbellifers, thistles and geophytes are widespread and result from degradation of the maquis and garigue, due to grazing and browsing and from soil erosion due to the short but heavy rainstorms which are characteristic of the islands. Some steppic communities are, however, climactic or semi-climactic with *Lygeum spartum* on clay slopes, or with *Hyparrhenia hirta* and *Andropogon distachyus*. Other steppes are characterised by *Brachypodium retusum* or, rarely, by *Phalaris truncata*. The more degraded steppes are characterised by *Stipa capensis* and *Aegilops geniculata* and a variety of thistles (e.g., *Carlina involucrata*, *Notobasis syriaca*, *Galactites tomentosa*) and geophytes (e.g., *Asphodelus aestivus*, and *Urginea pancration*). Steppic communities also develop on abandoned agricultural land, which is increasing in extent.

Habitats that are not part of the successional sequence include coastal marshlands, sand dunes, maritime vegetation, freshwater, and rupestral communities.

Maltese coastal marshes are characterized by a muddy substratum on which a pool of brackish water collects in the wet season. During the dry season this water becomes progressively more brackish until it finally disappears completely, leaving the marsh dry until the following wet season.

Many local sandy beaches were backed by dune systems, but at present only very few persist and even these have been much degraded mainly due to human activities in connection with beach development for touristic purposes and recreational use. Sand dune ecosystems are thus amongst the rarest and most threatened of local ecosystems. Local dunes are dominated by the dune grasses *Elytrigia juncea* and *Sporobolus pungens*, and, until recently, also by *Ammophila littoralis* which has now been totally extirpated.

On gently sloping rocky shores halophytic vegetation grows in isolated patches on the shallow saline soil that accumulates in pockets of the rock. The species present form part of the Mediterranean vegetational community called the *Crithmo-Limonietum*.

Rupestral assemblages dominated by shrubs occur on sheer rock faces and cliff/scree environments, mainly at the south, southwest and west coasts of the islands. Because of their relative inaccessibility these habitats provide important refuges for many species of Maltese flora and fauna, including many endemics, amongst which are two plant taxa (*Palaeocyanus crassifolius* and *Cremnophyton lanfrancoi*) belonging to monotypic genera.

The main freshwater habitats are those associated with valleys (in Maltese: *widien*), which are geomorphologically dry valleys, that is, valleys formed during a

previous climatic regime (the Pleistocene pluvial periods), which are now dry for some months of the year and in which water only flows during the wet season. However, some local *widien* drain springs originating from perched aquifers and retain some surface water even during the dry season. Other freshwater habitats are temporary rainwater pools, formed by rainwater that collects in natural depressions and hollows in rock during the wet season, and a few permanent ponds.

In spite of being made up almost exclusively of limestone, the Maltese Islands have surprisingly few known deep caves. Those caves that have been explored biologically have revealed an impoverished but interesting biota with a number of endemic invertebrates.

Because of the islands' high human population and considerable land use, anthropogenic habitats have a large coverage. Such habitats are dominated by a variety of plant species consisting mainly of ruderals and aliens. Different types occur in association with agriculture, afforestation, abandoned fields, along roadsides, in disturbed seaside habitats and in urban areas.

The above synthesis is based on Alexander (1988), Axiak *et al.* (2002), Bowen Jones *et al.* (1961), Chetcuti *et al.* (1992), Haslam *et al.* (1977), Lanfranco (1995), Pedley *et al.* (1976), Schembri (1993, 1997), Schembri *et al.* (1999), Schembri & Lanfranco (1993), and Vossmerbäumer (1972); these works should be consulted for more detail and for an extensive bibliography.

MATERIAL AND METHODS

The present paper is based on literature records that have been critically revised, and on unpublished material. For each species the following is reported: the scientific name; the complete name of the author and year of publication; the bibliographic references concerning the study area listed chronologically, with the name of the species and author as originally quoted; the general geographic distribution, mainly as a list of the countries or geopolitical units from where the species is known, critically revised from the literature; the chorotype according to Vigna Taglianti *et al.* (1992, 1999); the list of collecting sites for the species in the Maltese Islands, arranged according to island (Malta, Comino, Gozo), with the collecting sites for each island listed alphabetically; a synthesis of available data on habitat preferences in the study area; and taxonomic remarks where relevant.

The following acronyms are used for the collectors of the material examined and for the collections where this material is now deposited. Collectors: AD = A. Deidun; AV = A. Valle; CA = Causin; DC = D. Caruso; DJ = D.M. Johnson; EG = E.H. Giglioli; EL = E. Lanfranco; GT = G.B. Toscanelli; JS = J.L. Schembri; LM = L. Main; MG = M. Gauci; MP = M. Pace; PS = P.J. Schembri; SA = S. Azzopardi; SS = S. Schembri; ST = S. Saliba. Collections: AM = A. Minelli; BG = Museo Civico di Scienze naturali "E. Caffi", Bergamo, Italy; CT = Dipartimento di Zoologia, Università di Catania, Italy; DBUM = Department of Biology, University of Malta; FI = Museo di Storia naturale di Firenze, sezione Zoologica "La Specola"; MHNG = Muséum d'histoire naturelle, Genève; MZ = M. Zapparoli.

LIST OF THE SPECIES

SCUTIGEROMORPHA Gervais, 1837**SCUTIGERIDAE** Gervais, 1837***Scutigera*** Lamarck, 1801**1. *Scutigera coleoptrata*** (Linné, 1758)

Cermatia variegata Risso: Gulia, 1890: 41.

Cermatia variegata: Gulia, 1913: 554.

Scutigera coleoptrata: Schembri, 1996: 120.

Material examined. Malta: 1, Ballut ta' l-Imgiebah, 8.4.1984, PS (MZ, MZ det.); 1, Chadwick Lakes, 7.3.1975, DC (CT, AM det.); 1, G'Mangia, 1987, MG (MZ, MZ det.); 1, Malta, 5.1973, AV (BG, AM det.); 1, Manoel Island, 16.3.1985, PS (MZ, MZ det.); 1, S. Antonino [= San Anton Gardens], 12.3.1975, leg. ? (CT, AM det.); Siggiewi, 6.1982, MP (MZ, MZ det.).

General distribution. Portugal, Spain (incl. Balearic Is.), France (incl. Corsica), Italy (incl. Sardinia and Sicily), Switzerland, S. Germany, Austria, Czech Republic, Slovakia, S. Hungary, Slovenia, Croatia, Montenegro, FYR Macedonia, Albania, mainland and insular Greece (incl. Crete), Bulgaria, Romania, Ukraine (incl. Crimea), Caucasus, Near and Middle East, N. Africa (Egypt, Libya, Tunisia, Algeria, Morocco); also recorded from Madeira and the Canary Is. (introduced ?); introduced in Central and N. Europe, Asia, N. America, S. Africa, St. Helena, Argentina (Attems, 1907; Würmli, 1973, 1977).

Chorotype. Mediterranean (MED).

Ecological notes. Widespread species on the Maltese Islands, occurring in a range of habitats, usually with some degree of humidity, including human habitations and their surroundings (leaf litter, under thick vegetation, under stones on soil, in cellars etc).

LITHOBIOMORPHA Pocock, 1895**LITHOBIIDAE** Newport, 1844***Eupolybothrus*** Verhoeff, 1907Subgenus ***Allopolybothrus*** Verhoeff, 1907**2. *Eupolybothrus (Allopolybothrus) nudicornis*** (Gervais, 1837)

Eupolybothrus elongatus (Newp.): Matic et al., 1967: 197.

Material examined. Malta: 7, Attard, 5.3.1975 (CT, AM det.); 1 ♂, Bahrija Valley, 25.3.1984, PS & SS (DBUM, MZ det.); 1 ♀, Bingemma Gap, 24.3.1984, SS (MHNG, MZ det.); 1, Birkirkara, 10.1969, CA (MZ, MZ det.); 1, Buskett, 12.1.1980, PS (MZ, MZ det.); 1, Chadwick Lakes, 23.4.1983, PS (MZ, MZ det.); 1, Ghadira, 27.12.1979, PS (MZ, MZ det.); 1 juv., Ghajn Hadid, Selmun, 5.12.1983, MG (MHNG, MZ det.); 1, Ghar Lapsi, 6.3.1975, DC (CT, AM det.); 2, Malta, 2.3.1975, leg. ? (CT, AM det.); 4 ♂, 1 ♀, 1 ♀ juv., Manoel Island, 16.3.1985, PS (MZ, MZ det.); 1, Mistra Bay, 3.3.1975, DC (CT, AM det.); 1 ♂, Rabat, St. Agatha's Catacombs, 16.7.1984, MG (MHNG, MZ det.); 2 ♂, San Pawl tat-Targa, garden, pitfall trap, 17.2.1985, DJ (DBUM, MZ det.); 1 ♀, Tal-Kortin, Mistra, 18.3.1984, PS (MZ, MZ det.); 2 ♂, 1 ♀, Tal-Qroqq, UOM, under stones, *Acacia* stand, 27.3.1984, SA & LM (MZ, MZ det.); 4 ♂, 1 ♀, ibidem, pitfall trap, *Acacia* stand, 5.4.1984, SA & LM (MHNG, MZ det.); 5 ♂, 2 ♀, ibidem, carob, under stones, 16.4.1984, SA & LM (MZ, MZ det.); exx., Targa Gap, 10.1.1970,

leg.?; 3 juv., Wied Anglu, under stones, in watercourse, 16.12.1984, PS (MHNG, MZ det.); 2, Wied Babu, 23.5.1985, SS (MZ, MZ det.); exx., Wied Hassabtan, 20.1.1970, leg.? (MZ, MZ det.); 2 ♂, 1 ♀, Wied Incita, 25.3.1984, PS & SS (DBUM, MZ det.); 1, Wied is-Sewda, 26.3.1975, SS (MZ, MZ det.); 1 ♂ juv., 2 ♀ juv., Wied il-Ghasel, Mosta, garigue, under stones, 26.1.1985, PS (DBUM, MZ det.). Gozo: 1, Dwejra, 7.3.1975, DC (CT, AM det.); 1 ♀ juv., 1 imm., limits of Gharb, 14.2.1985, PS (MHNG, MZ det.); 1, Qala, 13.3.1975, DC (CT, AM det.); 2 ♀ juv., Wied il-Mielah, 16.2.1985, PS (DBUM, MZ det.).

General distribution. SE. France (Basses Alpes, Alpes Maritimes), Corsica, Italy (Apennines), Sardinia, Sicily, Malta, NE. Morocco, N. Tunisia, N. Algeria (Brölemann, 1921, 1930; Foddai *et al.*, 1995; Matic *et al.*, 1967; Zapparoli, 1984). Reported also from Spain by Attems (1927, 1952), but record needs to be confirmed.

Chorotype. W-Mediterranean (WME).

Remarks. The old records of Gulia (1890, 1913) quoted under *Lithobius forficatus* (Linnaeus, 1758) may refer to this species (see below).

Ecological notes. Common and widespread species on the Maltese Islands, occurring in a range of habitats that include *widien*, leaf litter under trees such as *Acacia* and *Ceratonia siliqua*, under stones in garigue, coastal vegetation, gardens and urbanised areas.

Lithobius Leach, 1814

Subgenus *Lithobius* Leach, 1814

3. *Lithobius (Lithobius) castaneus* Newport, 1844

Material examined. Malta: 1 ♀, Ghajn Rihana, 25.3.1984, PS (MHNG, MZ det.); 1, Malta, 2.3.1975, DC (CT, AM det.); 1, Malta, 5.4.1978, leg.? (MZ, MZ det.); 1, Il-Maqluba, 20.1.1980, SS (MZ, MZ det.); 1, ibidem, 14.2.1982, PS (MZ, MZ det.); 1 ♂ juv., San Pawl tat-Targa, garden, pitfall trap, 3.2.1985, DJ (MHNG, MZ det.); 1 ♂, 1 ♀, Tal-Qroqq, UOM, under stones, *Acacia* stand, 27.3.1984, SA & LM (DBUM, MZ det.); 3, ibidem, pitfall trap, *Acacia* stand, 5.4.1984, SA & LM (MZ, MZ det.); 6 ♀, ibidem, carob, under stones, 16.4.1984, SA & LM (MZ, MZ det.); 1 ♀, Wied Babu, 23.5.1985, SS (MHNG, MZ det.); 1 ♀, Wied l-Ghasel, Mosta, garigue, under stones, 26.1.1985, PS (DBUM, MZ det.).

General distribution. Morocco, Tunisia, Algeria, Portugal, Spain, France (incl. Corsica), Italy (including Sardinia and Sicily), Malta, S. Austria, Slovenia, Croatia, Bosnia Herzegovina, Serbia (Brölemann, 1921, 1930, 1932; Eason, 1982; Foddai *et al.*, 1995; Kos, 1992; Machado, 1952; Matic *et al.*, 1967; Stoev, 1997; Zapparoli, 1981); the species has been reported from Bulgaria, but records require confirmation (Stoev, 2002); introduced in Guatemala (Eason, 1973).

Chorotype. S-European (SEU).

Ecological notes. Common and widespread; occurring in a variety of habitats including *widien*, leaf litter under trees, under stones in garigue, and in gardens.

4. *Lithobius (Lithobius) forficatus* (Linnaeus, 1758)

Lithobius forficatus Leach [sic]: Gulia, 1890: 41.

Lithobius forficatus: Gulia, 1913: 554.

Material examined. No material from Malta examined (cf. Remarks).

General distribution. Iceland (introduced), Finland, Norway, Sweden, Denmark, United Kingdom, Ireland, Netherlands, France (incl. Corsica, but introduced),

Germany, Poland, Czech Republic, Slovakia, Hungary, Switzerland, Austria, Italy (incl. Sardinia and Sicily (Eolian Is.)), but introduced in both), Slovenia, Croatia, Bosnia Herzegovina, Serbia, Montenegro, FYR Macedonia, Romania, Bulgaria, Albania, mainland Greece, N. Turkey, Georgia, Russia (Krasnodar Prov.); also present in N. Africa (introduced?) and in Malta (introduced); from the W-Palearctic it has been introduced to N. America, S. America, St. Helena, Hawaii Is. (established?), Kuriles (Brölemann, 1930; Eason, 1964, 1970, 1982, 1996; Enghoff, 1983; Foddai *et al.*, 1995; Kos, 1992; Országh, 2001; Stoev, 1997; Tajovský, 2001; Wytwer, 1997; Zaleskaja, 1978; Zapparoli, 1999).

Chorotype. European (EUR).

Remarks. According to Zapparoli (1995a) this species has a very limited distribution in the micro- and macro-insular systems of the Mediterranean area, although it is highly anthropophilous. *L. forficatus* has never been recorded from the Balearic Is., Corsica, Sardinia, Sicily, Crete and Cyprus, from where it must be considered absent. In the Tyrrhenian area only a few records from Capri, the Eolian Is. (Lipari, Vulcano) and Lampedusa are known, all probably resulting from anthropic introductions. The only record of this species from the Maltese Islands is that of Gulia (1890, 1913), however, in spite of the in-depth research carried out no new records have been added since the end of the 19th century and we suspect that Gulia's record from Malta may be based on a misidentification and probably refers to another lithobiid species (possibly *E. nudicornis*?).

Ecological notes. No data available.

5. *Lithobius (Lithobius) lapidicola* Meinert, 1872

Material examined. Malta: 1 ♂, Buskett, leaf litter on tree, 30.12.1978, SS (MZ, MZ det.); 4 ♂, 3 ♀, Sliema, 22/23.12.1969, EL (MZ, MZ det.).

General distribution. Canary Is., Ireland, United Kingdom, Sweden, Netherlands, Germany, Switzerland, Denmark, Poland, Czech Republic, Slovakia, Ukraine, France (incl. Corsica), Italy (incl. Sardinia and Sicily), Austria, Hungary, Slovenia, Bosnia Herzegovina, Montenegro, Romania, Albania, mainland Greece (incl. Ionian Is.) (Brölemann, 1930; Eason, 1964, 1970, 1982, 1985, 1996; Enghoff, 1983; Foddai *et al.*, 1995, 1996; Kos, 1992; Országh, 2001; Stoev, 1997; Tajovský, 2001; Wytwer, 1997; Zaleskaja, 1978).

Chorotype. European (EUR).

Ecological notes. Records available at present indicate that this is a leaf litter species which occurs in semi-natural wooded areas (Buskett) and in urban gardens (Sliema).

6. *Lithobius (Lithobius) peregrinus* Latzel, 1880

Material examined. Malta: 1 ♂, Malta, date?, SS (MZ, MZ det.).

General distribution. SE. Italy (Gargano), Bosnia Herzegovina, Montenegro, FYR Macedonia, Albania, mainland Greece (incl. Ionian Is.), Bulgaria, Caucasus; introduced in the United Kingdom, France, Spain, NE. Italy, S. Africa, Bermuda Is., Panama (Stoev, 1997, 2001; Zapparoli, 1992).

Chorotype. S-European (SEU).

Remarks. There are no previous records of this species from Malta, were it has probably been introduced.

Ecological notes. No data available.

7. *Lithobius (Lithobius) trinacrius* Verhoeff, 1925

Material examined. Malta: 1 ♂, Ballut ta' l-Imgiebah, 8.4.1984, PS (MHNG, MZ det.); 1 ♂, Ghajn Hadid, 8.5.1983, PS (MZ, MZ det.); 1 ♀, Ghajn Hadid, Selmun, 5.12.1983, MG (MHNG, MZ det.); 1 ♀, 2 juv., Selmun, 5.2.1983, PS (MZ, MZ det.); 2 ♂, 2 ♀, Mgiebah, 9.11.1985, leg. ? (MZ, MZ det.). Gozo: 1 ♂, Dwejra, 9.2.1984, MG (MHNG, MZ det.); 1 ♂, 1 ♀, Ramla, 15.2.1986, clay slopes, PS (DBUM, MZ det.); 1 ♂, Xlendi, 26.4.1984, MG (MZ, MZ det.).

General distribution. Sicily (Foddai *et al.*, 1995); also reported from Pantelleria (Zapparoli, 1995a).

Chorotype. W-Mediterranean (WME).

Ecological notes. Available records indicate that this species has a distribution limited to coastal areas where it occurs under trees, shrubs, in grass steppes, on clay slopes and under maritime vegetation.

Subgenus *Monotarsobius* Verhoeff, 1905

8. *Lithobius (Monotarsobius) crassipes* L. Koch, 1862

Material examined. Malta: 2 ♂, Ballut tal-Wardija, soil and leaf litter, Berlese extractor, 8.4.1984, PS & SS (MZ, MZ det.); 1 ♂, 1 ♀, Nadur, near Bingemma Gap, 30.12.1984, PS (MHNG, MZ det.); 1 ♀, Wied Qannotta, S.E. end, 11.12.1983, PS (DBUM, MZ det.); 1 ♂ juv., Wied l-Ghasel, Mosta, 26.1.1985, PS (DBUM, MZ det.); 1 ♂, Wied il-Faham, 27.2.1982, PS (MZ, MZ det.). Gozo: 2 ♂, 5 ♀, limits of Kercem, 14.2.1985, PS (MZ, MZ det.); 1 ♂, Ta' Cenc, 2.2.1985, PS & MG (MHNG, MZ det.); 1 ♂, 1 ♀ juv., Wied ic-Cawla, 9.4.1984, MG (MZ, MZ det.); 3 ♂, 1 ♀, Wied il-Mielah, 16.2.1985, PS (MZ, MZ det.).

General distribution. Scandinavia, United Kingdom, Ireland, Iberia, France, Netherlands, Germany, Switzerland, Poland, Czech Republic, Slovakia, Austria, Italy (incl. Sardinia and Sicily), Slovenia, Croatia, Bosnia Herzegovina, Montenegro, Serbia, Albania, FYR Macedonia, mainland and insular Greece (incl. Crete), Bulgaria, Romania, Russia, Turkey, Syria, Jordan, Central Asia, Algeria, Tunisia, Canary Is., Madeira; probably introduced in N. America (Brölemann, 1921, 1930, 1932; Eason, 1964, 1982, 1985; Foddai *et al.*, 1995; Kos, 1992; Matic *et al.*, 1967; Országh, 2001; Stoev, 1997, 2001; Tajovský, 2001; Wytwer, 1997; Zaleskaja, 1978; Zapparoli, 1991, 1999).

Chorotype. W-Palaearctic (WPA).

Ecological notes. Common and quite widespread; this species occurs in soil and leaf litter beneath trees and shrubs, especially in sheltered situations, such as maquis in the deeper *widien*.

SCOLOPENDROMORPHA Pocock, 1895

SCOLOPENDRIDAE Newport, 1844

Scolopendra Linné, 1758

9. *Scolopendra cingulata* Latreille, 1829

Scolopendra cingulata Latr.: Gulia, 1890: 41.

Scolopendra cingulata: Gulia, 1913: 554.

Scolopendra cingulata Latr.: Matic *et al.*, 1967: 197.

Scolopendra cingulata: Schembri, 1996: 120.

Material examined. Malta: 1, Wied Mejxu, under stones, 25.10.1970, EL (MZ det.); 1, Birkirkara, under stones, 5.11.1974, SS (MZ det.). Comino: 2, under stones, 23.03.1975, SS (MZ det.); 1, Santa Marija Bay, 26.9.1982, PS (MZ, MZ det.).

General distribution. Tunisia, Algeria, Morocco, Portugal, Spain, France, Italy, Slovenia, Croatia, Bosnia Herzegovina, Serbia, Montenegro, FYR Macedonia, Romania, Bulgaria, Albania, mainland and insular Greece, Turkey, Hungary, Ukraine, S. European Russia (Crimea, Caucasus), NW Iran, Syria, Lebanon, Palestine, Israel, Jordan, Egypt (Sinai), Cyrenaica; also in Sicily and Cyprus; absent in Balearic Is., Corsica, Sardinia and Crete (Attems, 1930; Brölemann, 1921, 1930, 1932; Foddai *et al.*, 1995; Kos, 1992; Lewis, 1985; Serra, 1983; Stoev, 1997; Zaleskaja & Schileyko, 1992; Zapparoli, 1991, 1999). Two records from Tadjikistan (Zaleskaja & Schileyko, 1992).

Chorotype. (Turano?)-Mediterranean (MED).

Remarks. Recorded from many localities on Malta, as well as from the islands of Comino and Gozo (Matic *et al.*, 1967); many more specimens were seen by one of us (PS) but were not collected.

Ecological notes. Widespread species on the Maltese Islands, occurring in a wide range of habitats including coastal garigue and clay slopes, *widien*, inland garigue and fields.

10. *Scolopendra oraniensis* Lucas, 1846

Scolopendra canidens oraniensis (Luc.) [sic]: Matic *et al.*, 1967: 197.

Material examined. Malta: 1, Attard, 5.3.1975, leg. ? (CT, AM det.); 1, Bahrija Valley, 6.4.1985, PS (MZ, MZ det.); 1, Ghadira, 4.3.1975, leg. ? (CT, AM det.); 1, Ghajn Tuffieha, clay slopes, 24.2.1985, SS (MZ, MZ det.); 1, Ghar Lapsi, 6.3.1975, DC (CT, AM det.); 1, Gnejna, 10.4.1982, JS (DBUM, MZ det.); 1, Il-Fawwara, Dingli cliffs, 9.4.1983, SP (MZ, MZ det.); 1, Salina, 5.5.1984, SS (MZ, MZ det.); 1, Mgiebah Bay, clay slopes, 8.4.1984, PS (MZ, MZ det.); 1, Mistra, 3.3.1975, DC (CT, AM det.); 1, Wardija, 2.3.1975, leg. ? (CT, AM det.); 1, Wied Bufula, 8.11.1986, leg. ? (MZ, MZ det.); 1, Wied Incita, 25.3.1984, PS & SS (DBUM, MZ det.); 1, Wied l-Ghasel, Mosta, garigue, under stones, 26.1.1985, PS (MZ, MZ det.); 1, Wied Znuber, 15.4.1984, PS (MHNG, MZ det.); 1, Xrobb l-Ghagin, 7.5.1984, MG (MHNG, MZ det.). Gozo: 1, Dwejra, 17.5.1984, SS (MHNG, MZ det.); 2, Hondoq ir-Rummien, 5.3.1984, SS (DBUM, MZ det.); 1, Wied il-Mielah, 9.4.1984, MG (MZ, MZ det.).

General distribution. Portugal, Spain (incl. Balearic Is.), S. France, Corsica, Central and S. Italy, Sardinia, Sicily, Malta. Records from Morocco and Algeria are also known (Würmli, 1980).

Chorotype. Western Mediterranean (WME).

Ecological notes. Common and widespread especially in coastal areas; it occurs in *widien*, garigue and on clay slopes.

CRYPTOPIDAE Kohlrausch, 1881

Cryptops Leach, 1815

11. *Cryptops trisulcatus* Brölemann, 1902

Cryptops trisulcatus Brol. [sic]: Matic *et al.*, 1967: 197.

Material examined. Malta: 1, Chadwick Lakes, 7.3.1975, DC (CT, AM det.); 1, Ghadira, 4.3.1975, DC (CT, AM det.). Gozo: 1, Dwejra, 9.11.1984, MG (MZ, MZ det.); 1, ibidem, 17.5.1984, SS (MZ, MZ det.). Comino: 1, central area, 26.9.1982, PS (MZ, MZ det.).

General distribution. Canary Is., Algeria, Portugal, Spain (incl. Balearic Is.), S. France (incl. Corsica), Italy (Apenninic), Sardinia, Sicily, Romania, insular Greece (Ionian Is., S. Sporades, Crete), SE. Turkey (Attems, 1930; Brölemann, 1921, 1930, 1932; Foddai *et al.*, 1995, 1996; Machado, 1952; Negrea & Matic, 1973; Stoev, 1997; Zapparoli, 1999).

Chorotype. Mediterranean (MED).

Ecological notes. Available records suggest that this species has a rather limited distribution and occurs mostly in coastal areas, but also in *widien* (Chadwick Lakes).

GEOPHILOMORPHA Leach, 1815

HIMANTARIIDAE Cook, 1895

Himantarium C. Koch, 1847

12. *Himantarium gabrielis* (Linnaeus, 1767)

Himantarium gabrielis: Schembri, 1996: 120.

Material examined. Malta: 1, Ballut ta' l-Imgiebah, 8.4.1984, SS (MZ, MZ det.); 1, Ballut tal-Wardija, 8.4.1984, PS (MHNG, MZ det.); 1, Borg in-Nadur, B' Bugia, 20.1.1985, PS (MZ, MZ det.); 1, Il-Maqluba, Qrendi, 7.12.1982, PS (MHNG, MZ det.); 3, Malta, 12.1972/1.1973, AV (BG, AM det.); 1, San Pawl tat-Targa, 3.1983, DJ (MZ, MZ det.); 1, San Pawl tat-Targa, garden, pitfall trap, 17.2.1985, DJ (MHNG, MZ det.); 1, Tà Hammud, Mithleeb, 18.2.1983, PS (MZ, MZ det.); 1, Tal-Qroqq, UOM, 16.4.1984, SA & LM (MHNG, MZ det.); 1, Wied Anglu, 16.12.1984, PS (DBUM, MZ det.); 1, Wied Bufula, 8.11.1986, leg. ? (MZ, MZ det.).

General distribution. Tunisia, Algeria, Morocco, S. France (incl. Corsica), Italy (incl. Sardinia and Sicily), Slovenia, Croatia, Bosnia Herzegovina, Montenegro, FYR Macedonia, Albania, mainland and insular Greece (excl. Crete), S. Romania, Bulgaria, W. Turkey; introduced in Madagascar (Attems, 1929; Brölemann, 1921, 1930, 1932; Foddai *et al.*, 1995; Kos, 1992; Minelli *et al.*, 1984; Stoev, 1997, 2001; Zapparoli, 1999). Reported from Portugal by Attems (1929) but not by Machado (1952); also occurring in Central Europe (Brölemann, 1930).

Chorotype. Mediterranean (MED).

Ecological notes. Common and widespread species on the Maltese Islands, occurring in a wide range of habitats that include leaf litter under trees and shrubs, soil in garigue, *widien* and gardens.

Stigmatogaster Latzel, 1880

13. *Stigmatogaster gracilis* (Meinert, 1870)

Material examined. Malta: 2, 12.1972/1.1973, AV (BG, AM det.); 2, Malta, 8.1878, EG (FI, AM det.).

General distribution. Tunisia, Algeria, Balearic Is., S. France (incl. Corsica), Italy (incl. Sardinia and Sicily), Croatia, Montenegro, Albania, mainland and insular

Greece (excl. Crete) (Brölemann, 1921, 1930, 1932; Foddai *et al.*, 1995; Kos, 1992; Negrea & Matic, 1973; Stoev, 1997).

Chorotype. Mediterranean (MED).

Ecological notes. No data available.

***Bothriogaster* Sseliwanoff, 1879**

14. *Bothriogaster signata* (Kessler, 1874)

Bothriogaster signata Att. [sic]: Matic *et al.*, 1967: 196.

Material examined. Malta: 3, Tal-Qroqq, UOM, *Acacia* stand, under stones, 27.3.1984, SA & LM (MZ, MZ det.). Gozo: 2, Dwejra, 17.5.1984, SS (DBUM, MZ det.); 1, Qala, 17.5.1985, MG (MHNG, MZ det.).

General distribution. FYR Macedonia, Albania, Bulgaria, mainland and insular Greece (incl. Crete), Turkey, Cyprus, Syria, Palestine, Israel, Egypt, Libya (Cyrenaica, Tripolitania), Tunisia, Caucasus, Iran, Iraq, Jordan, Saudi Arabia, Turkestan, Usbekistan (Stoev, 2000; Zapparoli, 1991).

Chorotype. Turano-Mediterranean (TUM).

Remarks. Previously recorded from several localities on the island of Malta, as well as from Comino and Gozo (Matic *et al.*, 1967).

Ecological notes. Only few records are available but the species seems to prefer soil under vegetation in rather arid situations.

DIGNATHODONTIDAE Cook, 1895

***Dignathodon* Meinert, 1870**

15. *Dignathodon microcephalus* (Lucas, 1846)

Dignathodon microcephalum [sic] (Luc.): Matic *et al.*, 1967: 197.

Material examined. Malta: 2, Targa Gap, 2.10.1982, PS & SS (MZ, MZ det.).

General distribution. Morocco, Algeria, Tunisia, Portugal, Spain (incl. Balearic Is.), S. France (incl. Corsica), Italy (incl. Sardinia and Sicily), Austria, Croatia, Bosnia Herzegovina, Serbia, Montenegro, Czech Republic, Slovakia, Romania, Bulgaria, Albania, mainland and insular Greece (incl. Crete), Near and Middle East, Crimea; also recorded from Luxembourg, where it was probably introduced (Attems, 1929; Brölemann, 1921, 1930, 1932; Dobroruka, 1956; Foddai *et al.*, 1995, 1996; Kos, 1992; Machado, 1952; Matic, 1972; Negrea & Matic, 1973; Országh, 2001; Stoev, 1997; Tajovský, 2001; Zapparoli, 1991, 1995b, 1999).

Chorotype. Mediterranean (MED).

Remarks. This species has been previously recorded from Gozo (Matic *et al.*, 1967).

Ecological notes. No data available.

***Henia* C.L. Koch, 1847**

Subgenus *Meinertia* Bollmann, 1893

16. *Henia (Meinertia) bicarinata* (Meinert, 1870)

Material examined. Malta: 1, Bahrija Valley, 25.3.1984, PS & SS (MHNG, MZ det.); 1, Buskett, soil, leaf litter, Berlese extractor, 30.4.1984, PS (MZ, MZ det.); 1, Chadwick Lakes, 7.3.1975, DC (AM, AM det.); 1, Fomm ir-Rih (cobble beach), October 2001, MG (AM, AM det.); 1, Fomm ir-Rih (cobble beach, on wrack), October 2001, MG (AM, AM det.); 1, Wied l-Ghasel, near Mosta Fort, 16.3.1985, PS (MHNG, MZ det.); 1, Manoel Island, 3.4.1984, MG (MZ, MZ det.); 2, Mgiebah, 17.3.1985, leg. ? (DBUM, MZ det.). Gozo: 1, Dwejra, 17.5.1984, SS (MZ, MZ det.); 1, Fort Chambray slopes, 3.2.1985, PS & MG (MHNG, MZ det.); 1, Ta' Cenc, 2.2.1985, PS & MG (DBUM, MZ det.); 1, Ta' Cenc, 11.3.1975, DC (AM, AM det.).

General distribution. Macaronesia, Maghreb, Iberia, France (incl. Corsica), Italy (peninsular regions, Sardinia and Sicily), Croatia, Bosnia Herzegovina, Slovakia, Hungary, Bulgaria, mainland and insular Greece (incl. Crete), Turkey, Caucasus (Minelli, 1982; Országh, 2001).

Chorotype. Mediterranean (MED).

Ecological notes. A more or less widespread species that occurs in coastal areas in stranded *Posidonia* debris on beaches, on coastal clay slopes and amongst coastal vegetation, but also inland in *widien*, in soil and leaf litter under trees and shrubs, and under stones in garigue.

Subgenus *Chaetechelyne* Meinert, 1870

17. *Henia (Chaetechelyne) vesuviana* (Newport, 1845)

Material examined. Malta: 4, Nadur, near Bingemma Gap, 30.12.1984, PS (MZ, MZ det.).

General distribution. Tunisia (?), Spain (?), S. France, Corsica (?), Switzerland, Italy (incl. Sardinia and Sicily), Croatia, Slovenia, SW. Romania (Minelli, 1982; Kos, 1992; Stoev, 1997).

Chorotype. Western Mediterranean (WME).

Ecological notes. The only locality where this species has been collected on the Maltese Islands has mainly a garigue and low maquis vegetation.

SCHENDYLIDAE Verhoeff, 1908

Schendyla Bergsoe & Meinert, 1866

18. *Schendyla* sp. n.

Material examined. Malta: 7, Ballut ta' l-Imgiebah, soil leaf litter, 8.4.1984, PS (MZ, MZ det.); 1, Nadur, near Bingemma Gap, 30.12.1984, PS (MZ, MZ det.); 1 ♀, Mtaħleb, 6.3.1975, DC (AM, AM det.).

Remarks. This new taxon will be described in the context of a revision of the Mediterranean *Schendyla* species.

Ecological notes. The specimens were found in soil and leaf litter under trees (*Quercus ilex* at Ballut ta' l-Imgiebah) and in low maquis (*Ceratonia siliqua* at Bingemma Gap).

GEOPHILIDAE Cook, 1895

Pachymerium C.L. Koch, 1847

19. *Pachymerium ferrugineum* (C.L. Koch, 1835)

Pachymerium ferrugineum (C. Koch) [sic]: Matic *et al.*, 1967: 197.

Material examined. Malta: 1, Ghadira, near reserve, 21.4.1984, PS (MHNG, MZ det.); 1, Girgenti, 18.10.1986, PS (MZ, MZ det.); 1, Malta, 8.10.1878, EG & GT (FI, AM det.); 1, Salina, 5.5.1984, SS (DBUM, MZ det.); 1, ibidem, 22.1.1985, MG (MZ, MZ det.); 2, San Pawl tat-Targa, garden, pitfall trap, 17.2.1985, DJ (MZ, MZ det.); 4, Tal-Qroqq, UOM, 5.4.1984, SA & LM (MZ, MZ det.); 1, Wied Bufula, 8.11.1986, leg. ? (DBUM, MZ det.); 1, Wied l-Ghasel, Mosta, 16.12.1983, PS (MHNG, MZ det.). Gozo: 1, Fort Chambray slopes, 3.2.1985, PS & MG (MHNG, MZ det.); 1, Qala, 17.5.1985, MG (MZ, MZ det.); 1, Ramla Dunes, 16.5.1984, SS (MZ, MZ det.); 1, Ramla, 4.3.1984, SS (MHNG, MZ det.); 1, ibidem, 2.2.1985, PS (MHNG, MZ det.); 2, ibidem, 15.2.1985, PS (MZ, MZ det.); 1, Ta' Cenc, 2.2.1985, PS & MG (MZ, MZ det.), 1, Xatt l-Ahmar, 4.5.2002, AD (AM, AM det.).

General distribution. Macaronesia (Azores, Madeira, Canary Is.), N. Africa (Tunisia; Algeria incl. Mediterranean coasts and Hoggar, Central Sahara; Morocco; Libya: Cyrenaica, Tripolitania), Portugal, Spain (incl. Balearic Is.), France (incl. Corsica), Italy (incl. Sardinia and Sicily), Austria, former Czechoslovakia, Poland, Latvia, Hungary, Slovenia, Croatia, Bosnia Herzegovina, FYR Macedonia, Albania, Bulgaria, Greece, Romania, European Russia, Turkey, Cyprus, Palestine, Iran, Caucasus, Turkestan; recorded from Scandinavia (Finland, Norway), United Kingdom, Netherlands; also present in Alaska and Pribilof Is.; introduced to Japan, Hawaii Is., N. America, Juan Fernández Is., Mexico, Easter I. (Barber, 1985; Eason, 1964; Meidell, 1977; Palmén & Rantala, 1954; Stoev, 2000).

Chorotype. W-Palearctic (WPA).

Ecological notes. Widespread species on the Maltese Islands, occurring in a wide range of habitats including coastal garigue and clay slopes, sandy beaches, *widien*, inland garigue and gardens.

***Clinopodes* C.L. Koch, 1847**

20. *Clinopodes flavidus* (C.L. Koch, 1847)

Material examined. Malta: 1, Buskett, 30.12.1978, B/2, JS (MZ, MZ det.).

General distribution. Poland, Czech Republic, Slovakia, Austria, Italy (incl. Sicily, excl. Sardinia), Slovenia, Croatia, Bosnia Herzegovina, Serbia, Montenegro, FYR Macedonia, Albania, Romania, Bulgaria, mainland and insular Greece (incl. Crete), Turkey, Cyprus, Palestine, Syria, European Russia, Crimea, Caucasus, Turkestan (Attems, 1929, 1949; Foddai *et al.*, 1995; Kos, 1992; Országh, 2001; Stoev, 1997, 2001; Wytwer, 1997; Tajovský, 2001; Zapparoli, 1995b, 1999).

Chorotype. Turano-European (TUE).

Ecological notes. The only locality from where this species was collected in the Maltese Islands is a semi-natural woodland.

***Tuoba* Chamberlin, 1920**

21. *Tuoba poseidonis* (Verhoeff, 1901)

Material examined. Malta: 4, Golden Bay, 19.11.2001, AD (AM, AM det.); 2, ibidem, 19.11.2001, AD (AM, AM det.). Gozo: 1, Xatt L-Ahmar, 1.5.2002, SS (AM, AM det.); 1, Xatt L-Ahmar, 1.5.2002, ST (AM, AM det.); 1, Xatt L-Ahmar, 1.5.2002, ST (AM, AM det.); 25, Xatt L-Ahmar, 4.5.2002, AD (AM, AM det.).

General distribution. Coasts of S. France (incl. Corsica), Central and S. Italy (incl. Sardinia and Sicily), Slovenia, mainland and insular Greece, Jordan (Dead Sea),

Egypt (Red Sea), Somalia (Indian Ocean) (Attems, 1929; Brölemann, 1930; Foddai *et al.*, 1995, 1996; Stoev, 1997; Zapparoli, 1990, 1991).

Chorotype. Mediterranean (MED).

Ecological notes. Found under stranded *Posidonia* debris on sandy beaches.

FAUNISTIC AND ZOOGEOGRAPHIC REMARKS

On the basis of the faunistic data available so far, twenty-one species of centipedes are here listed from the Maltese Archipelago, i.e. 1 Scutigermorpha, 7 Lithobiomorpha, 3 Scolopendromorpha, and 10 Geophilomorpha. Of these, 20 have been confirmed to occur on the island of Malta, 11 species on Gozo and three on Comino (Tab. I).

The faunistic data presented in this study are significant, since they are the result of systematic collecting made in different seasons over a number of years and employing different collecting methods, but it is likely that the real number of species present in the Maltese Islands is slightly higher than reported here.

One possible addition to the list may be *Cryptops punicus* Silvestri, 1896, a thermoxerophilous species widespread in the W-Mediterranean basin and known from the Tuscany Is. (Montecristo), Sardinia, Ustica, Sicily, Pantelleria, Lampedusa and Tunisia (cf. Zapparoli, 1995a).

Other species that can be expected to occur in the Maltese Archipelago are *Hydroschendyla submarina* (Grube, 1872) and *Nannophilus eximius* (Meinert, 1870). *H. submarina* is a halophilous species, with a Mediterranean-Atlantic distribution for which some records are known for the Tyrrhenian (Tuscany Is., NE. Sardinia, Campania, Linosa: Zapparoli, 1995a) and Aegean areas (Zapparoli, 2002). *N. eximius* is a W-Mediterranean element, recorded from Macaronesia (Madeira, Canary Is.), N. Africa (Algeria, Tunisia) and S. Italy (Sicily, Calabria, Basilicata, Puglia); it is also present in the circum-Sicilian micro-insular systems (Egadi Is., Eolian Is., Pelagian Is.).

Another species that may also be present is *Geophilus insculptus* Attems, 1895, a rather euryoecious geophilomorph widely distributed in Europe and also present in N-Africa. In the Tyrrhenian islands this species is known from many localities on Sardinia and Sicily and it has also been recorded from the Tuscany Is. (Giannutri, Giglio), Campane Is. (Ischia), Egadi Is., Eolian Is., Pantelleria and Lampedusa (Zapparoli, 1995a).

With respect to our knowledge of the centipede fauna of individual Maltese islands, data are most complete for Malta, while the number of species that occur on Gozo and Comino is very likely an underestimate. Some widespread Mediterranean elements (e.g.: *Scutigera coleoptrata*, *Eupolybothrus nudicornis*, *Lithobius crassipes*, *Scolopendra oraniensis*, *Pachymerium ferrugineum*, *Tuoba poseidonis*) have not been recorded from Gozo and Comino, probably due to inadequate collecting on these islands.

When compared to the faunas of the Central Mediterranean mainland and insular areas (Sicily, Eolian Is., Ustica, Egadi Is., Pantelleria, Linosa, Lampedusa and Tunisia), the centipede fauna of the Maltese Islands represents about a third of that

known to date for this region as a whole (Tab. II). However, faunistic knowledge of these areas is still incomplete. Best known are the Sicilian (including the small surrounding islands) and Maltese faunas, both of which have been the object of recent and repeated studies. Just under fifty species have been recorded from these localities as a whole (Foddai *et al.*, 1995, 1996). In contrast, knowledge of the centipedes of N. Africa, and particularly Tunisia, is much less complete and in need of updating. Some forty species have been recorded from this region to date, at least five of which are doubtful (Brölemann, 1921, 1932; Zapparoli, unpublished records).

Leaving out *L. peregrinus*, which is probably introduced, and *L. forficatus*, the presence of which on Malta is doubtful, almost 70% of the centipedes of the Maltese Islands are represented by species with a high dispersal ability. They are widespread in the Mediterranean area and are present in most of the aforementioned insular and mainland localities in the Central Mediterranean (Tabs II, III).

Apart from *Schendyla* n. sp., the remaining Maltese centipede species are more or less widely distributed but absent from N. Africa (*Lithobius lapidicola*, *L. trinacrius*, *Scolopendra oraniensis*, *Clinopodes flavidus*) or from southern Italy (*Bothriogaster signata*). For *Bothriogaster signata*, however, the possibility that its presence on Malta is a result of anthropic introduction cannot be excluded.

From a zoogeographic point of view, an analysis of the chorotypes represented in the study area (Tab. III) shows the Maltese centipede fauna to have a strong "Mediterranean" character, with this chorological element approaching 67%. This agrees well with the results of studies on the centipede fauna of other insular systems of the Sicily Channel (Pantelleria, Linosa, Lampedusa) (Zapparoli, 1995a). Species with a wide distribution in the Holarctic Region and in Europe are poorly represented (22% and 11% respectively).

Our studies on the centipede fauna of the Maltese Islands lead us to conclude that the composition of the fauna of these islands is affected mainly by ecological factors (the availability of suitable habitats) and by colonization-extinction events, rather than by paleogeographic and paleoclimatic factors. This is in accordance with the conclusions of previous studies on the centipedes of the W-Mediterranean micro-insular systems (Foddai *et al.*, 1996).

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TAB. I - Distribution of the centipedes recorded from the main islands of the Maltese Archipelago. Symbols: + = present; - = absent; ? = doubtful record; * = introduced or probably introduced species. Only confirmed species are considered in the total.

	Malta	Gozo	Comino
<i>Scutigera coleoptrata</i> (Linné, 1758)	+	-	-
<i>Eupolybothrus</i> (<i>Allopolybothrus</i>) <i>nudicornis</i> (Gervais, 1837)	+	+	-
<i>Lithobius</i> (<i>Lithobius</i>) <i>castaneus</i> Newport, 1844	+	-	-
<i>Lithobius</i> (<i>Lithobius</i>) <i>forficatus</i> (Linné, 1758)	?	-	-
<i>Lithobius</i> (<i>Lithobius</i>) <i>lapidicola</i> Meinert, 1872	+	-	-
<i>Lithobius</i> (<i>Lithobius</i>) <i>peregrinus</i> Latzel, 1880	*	-	-
<i>Lithobius</i> (<i>Lithobius</i>) <i>trinacrius</i> Verhoeff, 1925	+	+	-
<i>Lithobius</i> (<i>Monotarsobius</i>) <i>crassipes</i> L. Koch, 1862	+	+	-
<i>Scolopendra cingulata</i> Latreille, 1829	+	+	+
<i>Scolopendra oraniensis</i> Lucas, 1846	+	+	-
<i>Cryptops trisulcatus</i> Brölemann, 1902	+	+	+
<i>Himantarium gabrielis</i> (Linné, 1767)	+	-	-
<i>Stigmatogaster gracilis</i> (Meinert, 1870)	+	-	-
<i>Bothriogaster signata</i> (Kessler, 1874)	*	*	*
<i>Dignathodon microcephalus</i> (Lucas, 1846)	+	+	-
<i>Henia</i> (<i>Meinertia</i>) <i>bicarinata</i> (Meinert, 1870)	+	+	-
<i>Henia</i> (<i>Chaetechelyne</i>) <i>vesuviana</i> (Newport, 1845)	+	-	-
<i>Schendyla</i> sp. n.	+	-	-
<i>Pachymerium ferrugineum</i> (C.L. Koch, 1835)	+	+	-
<i>Clinopodes flavidus</i> C.L. Koch, 1847	+	-	-
<i>Tuoba poseidonis</i> (Verhoeff, 1901)	+	+	-
Total	20	11	3

	SIC	EOL	UST	EGA	PAN	MAL	LIN	LAM	TUN
<i>Scolopendra morsitans</i> Linné, 1758	-	-	-	-	-	-	-	-	*
<i>Scolopendra oraniensis</i> Lucas, 1846	+	+	+	+	-	+	-	-	-
<i>Cormocephalus gervaisianus</i> (C.L. Koch, 1841)	-	-	-	-	-	-	-	-	+
<i>Otostigmus spinicaudus</i> (Newport, 1844)	-	-	-	-	-	-	-	-	+
<i>Plutonium zwierleinii</i> Cavanna, 1881	+	-	-	-	-	-	-	-	-
<i>Cryptops anomalous</i> Newport, 1844	+	-	-	-	-	-	-	-	-
<i>Cryptops hortensis</i> Leach, 1815	+	-	-	-	-	-	-	-	-
<i>Cryptops numidicus</i> Lucas, 1846	+	-	-	-	-	-	-	-	?
<i>Cryptops punicus</i> (Silvestri, 1896)	+	-	+	-	-	-	-	+	+
<i>Cryptops trisulcatus</i> Brölemann, 1902	+	+	+	+	+	+	-	-	?
<i>Himantarium gabrielis</i> (Linné, 1767)	+	+	+	+	+	+	-	+	+
<i>Himantarium mediterraneum</i> (Meinert, 1870)	+	-	-	-	-	-	+	+	+
<i>Mesocanthus albus</i> Meinert, 1870	-	-	-	-	-	-	-	-	+
<i>Stigmatogaster dimidiatus</i> (Meinert, 1870)	+	+	-	-	+	-	-	+	+
<i>Stigmatogaster gracilis</i> (Meinert, 1870)	+	+	-	+	-	+	-	-	+
<i>Stigmatogaster superbus</i> (Meinert, 1870)	+	-	-	-	-	-	-	-	?
<i>Bothriogaster signata</i> (Kessler, 1874)	-	-	-	-	-	*	-	-	+
<i>Orya barbarica</i> (Gervais, 1835)	-	-	-	-	-	-	-	-	+
<i>Dignathodon microcephalus</i> (Lucas, 1846)	+	+	-	+	-	+	-	-	+
<i>Henia</i> (<i>Henia</i>) <i>pulchella</i> (Meinert, 1870)	+	-	-	-	-	-	-	-	+
<i>Henia</i> (<i>Meinertia</i>) <i>bicarinata</i> (Meinert, 1870)	+	+	-	+	+	+	+	+	+
<i>Henia</i> (<i>Pseudochaetehelne</i>) <i>brevis</i> (Silvestri, 1896)	-	-	-	-	+	-	-	-	-
<i>Henia</i> (<i>Chaetehelne</i>) <i>vesuviana</i> (Newport, 1845)	+	+	-	-	+	+	-	-	+
<i>Hydroschendyla submarina</i> (Grube, 1872)	+	+	-	+	-	-	+	-	-
<i>Haploschendyla barbarica</i> (Meinert, 1870)	?	-	-	-	-	-	-	-	+
<i>Nannophilus eximius</i> (Meinert, 1870)	+	+	-	+	+	-	+	+	+
<i>Schendyla mediterranea</i> Silvestri, 1897	+	-	-	-	-	-	-	-	-
<i>Schendyla monoei</i> Brölemann, 1904	+	-	-	-	-	-	-	-	-
<i>Schendyla montana</i> (Attems, 1895)	-	-	-	-	+	-	-	-	?
<i>Schendyla nemorensis</i> (C.L. Koch, 1836)	+	+	-	-	-	-	-	-	+
<i>Schendyla</i> n. sp.	-	-	-	-	-	-	-	-	-
<i>Pachymerium ferrugineum</i> (C.L. Koch, 1835)	+	+	-	+	+	+	+	+	+
<i>Gnathoribautia bonensis</i> (Meinert, 1870)	+	-	-	-	-	-	-	-	+

	SIC	EOL	UST	EGA	PAN	MAL	LIN	LAM	TUN
<i>Clinopodes flavidus</i> C.L. Koch, 1847	+	+	-	+	-	+	-	-	-
<i>Geophilus carpophagus</i> Leach, 1815	+	+	-	+	+	-	-	-	+
<i>Geophilus flavus</i> (DeGeer, 1778)	+	-	-	-	-	-	-	-	+
<i>Geophilus insculptus</i> Attems, 1895	+	-	-	-	+	-	-	+	?
<i>Geophilus linearis</i> C.L. Koch, 1835	-	-	-	+	-	-	-	-	-
<i>Geophilus osquidatum</i> Brölemann, 1909	+	-	-	-	-	-	-	-	-
<i>Geophilus piae</i> Minelli, 1983	+	-	-	-	-	-	-	-	-
<i>Geophilus pusillus</i> (Meinert, 1870)	-	-	-	-	-	-	-	-	+
<i>Geophilus richardi</i> (Brölemann, 1904)	+	-	-	-	-	-	-	-	-
<i>Geophilus truncorum</i> (Bergsoe & Meinert, 1866)	-	-	-	-	-	-	-	-	+
<i>Sinophilus frenum</i> Silvestri, 1896	-	-	-	-	-	-	-	-	+
<i>Tuoba poseidonis</i> (Verhoeff, 1901)	+	+	-	+	-	+	-	+	?
<i>Strigamia acuminata</i> (Leach, 1815)	+	-	-	-	-	-	-	-	-
Total	48	25	7	20	18	20	8	17	35

TAB. III - Chorological spectrum of the Maltese centipedes; *Lithobius forficatus* (Linné, 1758), *L. peregrinus* Latzel, 1880 and *Schendyla* n. sp. are not included; number of species and percentage frequency for each chorotype class and chorotype are given in parentheses.

Chorotype class (n. of spp. ; %)	Chorotypes (n. of spp. ; %)	Species
<i>Species widely distributed in Holoarctic Region</i> (4; 22.2)	W-Palaeartic (2; 11.1)	<i>Lithobius crassipes</i> L. Koch, 1862 <i>Pachymerium ferrugineum</i> (C.L. Koch, 1835) <i>Clinopodes flavidus</i> C.L. Koch, 1847 <i>Bothriogaster signata</i> (Kessler, 1874)
	Turano-European (1; 5.5)	
	Turano-Mediterranean (1; 5.5)	
<i>Species widely distributed in Europe</i> (2; 11.1)	European (1; 5.5)	<i>Lithobius lapidicola</i> Meinert, 1872
	S-European (1; 5.5)	<i>Lithobius castaneus</i> Newport, 1844
<i>Species widely distributed in the Mediterranean area</i> (12; 66.6)	Mediterranean (8; 44.4)	<i>Scutigera coleoptrata</i> (Linné, 1758) <i>Scolopendra cingulata</i> Latreille, 1829 <i>Cryptops trisulcatus</i> Brölemann, 1902 <i>Himantarium gabrielis</i> (Linné, 1767) <i>Stigmatogaster gracilis</i> (Meinert, 1870) <i>Dignathodon microcephalus</i> (Lucas, 1846) <i>Henia bicarinata</i> (Meinert, 1870) <i>Tuoba poseidonis</i> (Verhoeff, 1901) <i>Eupolybothrus nudicornis</i> (Gervais, 1837) <i>Lithobius trinacrius</i> Verhoeff, 1925 <i>Scolopendra orantiensis</i> Lucas, 1846 <i>Henia vesuviana</i> (Newport, 1845)
	W-Mediterranean (4; 22.2)	

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